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CONTENTS

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VARIATIONS IN THE VENATION OF *GLOSSINA* WIEDEMANN (DIPTERA : MUSCIDAE)

By J. P. Glasgow

*(East African Trypanosomiasis Research Organization, Tororo, Uganda)**

The wing venation of *Glossina* is constant in the ordinary sense throughout the genus. It has been figured by several authors, including Imms (1957) and Buxton (1955). Some individuals of *G. swynnertoni* Austen and of several, perhaps all, other species, have short supernumerary stub veins. These stub veins occur, not at random, but in a number of recognizable sites. It has been found convenient to distinguish the stubs occurring in different sites with letters of the alphabet, and the nomenclature adopted is shown in figure 1. Two other variants have been recognized but are not shown on figure 1. These are *g*, a gap in the fourth vein, between positions *b* and *k* in figure 1 ; and *h*, a gap in the cross-vein closing the " hatchet " cell distally, between positions *f* and *d* on figure 1.

Plate I presents photographs of wings which are abnormal, in some cases spectacularly so. Plate I, fig. 1, shows a result of the experiment, reported below, on the artificial induction of abnormalities by exposing puparia to high temperatures. The condition shown in Plate I, fig. 4, in which *b* and *c* are joined to form a supernumerary vein dividing the hatchet cell into two, is very rare in *G. swynnertoni*, having been observed in only four of about 30,000 individuals. In *G. palpalis fuscipes* Newstead it appears more common, having been seen twice in less than 2,000 individuals examined. One of these had the condition symmetrically in both wings, while the other *G. palpalis fuscipes* and all the four *G. swynnertoni* were asymmetrical, as shown in Plate I, fig. 4.

Table I.—*Occurrence of variations, as defined in figure* 1, *in male* G. swynnertoni *from Block* 9, *Shinyanga*

1953	*a*	*b*	*c*	*d*	*e*	*f*	*g*	*h*	*j*	*k*	*l*	Total	Temp. °C.	Number examined
May	.	.	.	.	.	.	.	.	.	.	.	.	24·54	.
June	.	.	.	.	.	.	.	.	.	.	.	.	24·79	.
July	9	9	1	1	39	2	0	0	2	0	1	64	22·46	1000
August	27	10	1	3	37	9	0	0	3	2	0	92	23·69	1000
September	21	11	0	3	38	4	0	0	1	1	0	79	24·55	1034
October	45	28	2	9	46	15	0	1	1	0	0	147	26·10	1000
November	87	65	3	5	68	9	0	0	5	3	0	245	26·19	1000
December	.	.	.	.	.	.	.	.	.	.	.	.	24·24	.
1954														
January	94	62	8	10	48	13	0	0	9	1	0	245	23·04	1000
February	32	13	0	1	20	6	0	0	6	0	2	80	24·50	1000
March	13	5	0	5	20	11	0	0	4	0	0	58	24·78	1000
April	13	5	3	6	28	8	0	0	8	0	0	71	23·45	1000
May	10	7	0	4	18	5	0	0	5	0	1	50	24·03	1000
June	11	6	0	1	23	3	0	0	8	0	0	52	23·09	1000
July	15	6	1	2	22	4	0	0	0	0	0	50	22·50	1000
August	21	9	1	1	31	12	0	0	2	0	0	77	23·35	1000
September	12	2	0	2	19	0	0	0	2	0	0	37	24·91	500
October	61	25	0	4	36	11	0	0	11	0	0	148	25·90	1000
November	132	103	24	25	74	24	0	0	15	6	2	405	26·13	1000

* This paper comes from the Entomological Research Laboratory, Shinyanga, Tanganyika.

Table I presents the occurrences observed in a monthly sample of about 1000 male *G. swynnertoni* between July 1953 and November 1954. Any particular variation can occur on the right wing, the left wing, or both, but any of these three possibilities is scored as one occurrence in Table I. Any particular tsetse can have more than one variation but such associated occurrences are recorded in Table I as their separate components. These samples were collected in the area of thorn-bush known as Block 9 at Shinyanga. The temperatures are half the sum of the mean maximum and mean

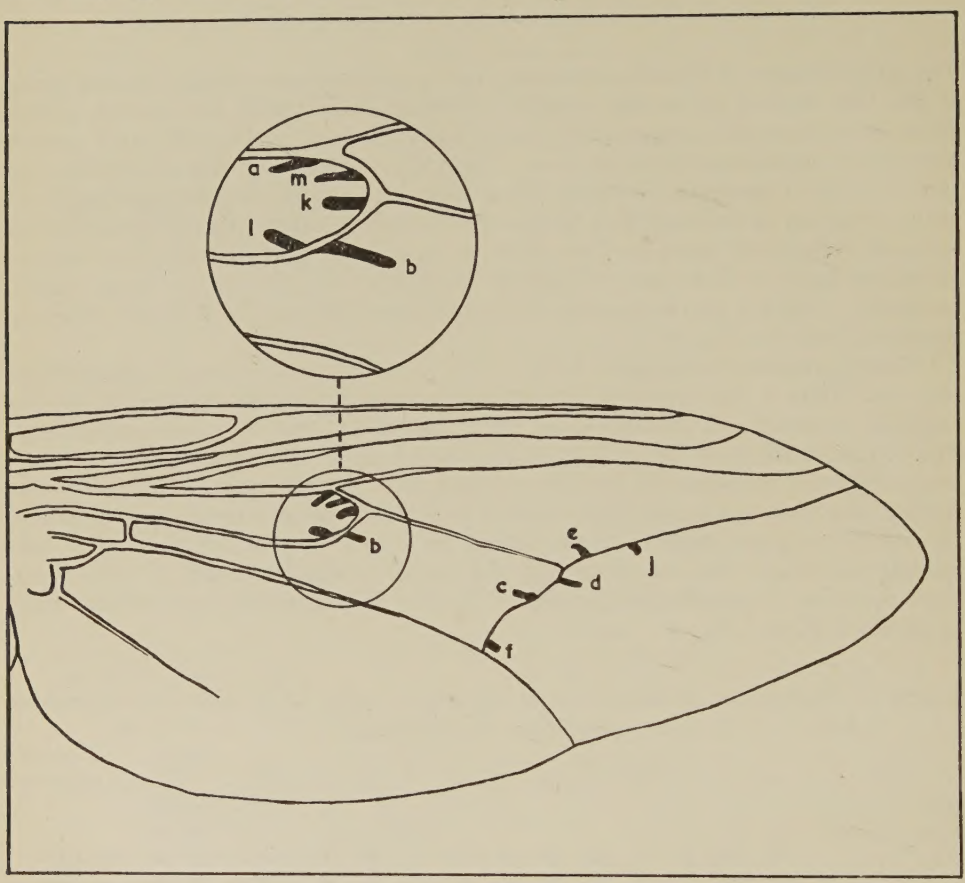

Fig. 1.—Diagram of variations, showing nomenclature adopted. The thickness of the anomalous stub veins has been exaggerated for clarity in the diagram, but they are in fact exactly similar in appearance to the regular veins.

minimum recorded at the laboratory some two miles south of the collecting area. It will be noticed that there are distinct seasonal changes, with the greatest abundance of variants shortly after the highest temperatures, suggesting that the temperature experienced by the pupae may be connected with the frequency of the variations. It is also noticeable that the seasonal effect is differential, in that *e* was commonest from March to September, but it was exceeded by *a* in the other months (except in October, 1953) in some of which it was also exceeded by *b*.

Sex Differences

At least some of the variations occur with differing frequency in the sexes, as shown in Table II. As female *G. swynnertoni* are more difficult to collect in large numbers than are males, the variations have been less studied in females. Table II

presents all the data available for female *G. swynnertoni*, together with comparable data for males which were collected at the same places and times by the same methods. On total occurrences, there is a significant excess of *e* and *f* in males, and of *a*, *b*, *c*, *d* and *k* in females.

TABLE II.—G. swynnertoni

a	*b*	*c*	*d*	*e*	*f*	*g*	*h*	*j*	*k*	*l*	*m*	Number examined	Details
							A. *Males*						
66	39	2	12	84	19	0	1	2	1	0	0	2034	September–October, 1953. Routine : wild, B. 9.
94	48	4	11	36	14	0	0	4	2	0	0	1252	Emerged from wild pupae, 16.xi.53–7.i.54.
22	34	2	5	22	3	0	0	0	1	0	0	477	Cold pupae. October–November, 1956.
19	33	3	1	20	4	0	0	2	1	0	0	407	Hot pupae. October–November, 1956.
16	49	9	4	9	9	0	0	2	2	0	0	90	Hot pupae. May, 1958.
217	203	20	33	171	49	0	1	10	7	0	0	4260	Totals.
51	48	5	8	40	12	0	0	2	2	0	0		Per thousand.
							B. *Females*						
86	42	10	12	6	3	0	0	0	4	0	0	1000	September–October, 1953. Wild, B. 9.
178	70	10	34	8	1	0	0	0	4	1	0	1356	Emerged from wild pupae, 16.xi.53–7.i.54.
72	46	2	13	7	6	0	0	2	3	0	0	458	Cold pupae. October–November, 1956.
43	42	6	9	7	3	0	0	1	6	0	2	347	Hot pupae. October–November, 1956.
19	47	6	1	2	5	0	0	2	4	0	0	60	Hot pupae. May, 1958.
398	247	34	69	30	18	0	0	5	21	1	2	3221	Totals.
124	77	11	21	9	6	0	0	2	7	0	1		Per thousand.

THE INHERITANCE OF THE VARIATIONS

It was thought that the characters being studied might be inherited as Mendelian recessives, and a breeding experiment was undertaken to test this possibility.

Since one mating can suffice a female tsetse for her whole life, it was necessary to use virgin females. Puparia of *G. swynnertoni* were collected in Block 9 at Shinyanga. Those emerging flies possessing atypical venation were separated each in a single 3 × 1-inch tube closed with cotton net at one end and a cork at the other. All matings were between individuals possessing the same variation. When an atypical female had been isolated, if no male of potent age with the same variation was available in the breeding stock, a search was made in Block 9 for a male with the same character. The flies were given an opportunity to feed on man every day. At the time of this experiment (November 1953) the importance of temperature to the characters being studied had not been realized ; also at that time we lacked constant-temperature rooms. The temperature of the experimental insects was, therefore, neither controlled nor recorded. The duration of the puparial period, however, was recorded, and varied between 22 and 28 days. Twenty-two days for a female puparium corresponds to a mean temperature of 28·7° C., and 28 days for a male to 26° C., according to the formula given by Jackson (1949). Since the male puparial period is longer, if the sexes were not as assumed the range of temperature must have been wider, but this seems improbable.

TABLE III.—*The results of mating* 11 *male and* 13 *female abnormal* G. swynnertoni. *Each parent is designated by an individual serial number and by one or two letters indicating the characters it possessed*

	Father	Mother	Offspring	Pupal period. days	Notes
a	1*a*	2*a*	Normal	24	No inheritance of *a*.
	8*a*	29*a*	Normal	26	.
	36*a*	35*a*	*f*	24	Siblings unlike each other, and unlike parents.
			b	24	
b	14*b*	15*ab*	Normal	23	*b* occurs in 8 of 11 offspring.
			ab	24	
	17*b*	18*b*	*b*	24	2 sets of siblings unlike, 2 alike.
			bd	28	
	19*b*	20*b*	*b*	26	.
			b	23	
			b	22	
	24*b*	23*b*	Normal	22	.
	33*b*	32*b*	*bf*	28	.
	33*b*	48*b*	*b*	24	.
			Normal	27	
d	10*d*	34*d*	Normal	24	*d* occurs in 1 of 5 offspring.
	10*d*	43*d*	*d*	23	Siblings unlike.
			Normal	26	
	50*d*	59*d*	*a*	24	.
	57*d*	56*ad*	Normal	23	.

Offspring were not sexed.
Assuming the 22 day ones were female, T was 28·7° C.
Assuming the 28 day ones were male, T was 26° C.
Duration of experiment: November–December, 1953.

Only 20 offspring in all were obtained from 11 fathers and 13 mothers, as shown in Table III. It had been expected that matings between like parents might produce offspring with the character in question particularly well developed; no such effect was observed. Results were obtained only in respect of the three characters *a*, *b* and *d*. In the case of *a* none of the four offspring exhibited the character, although in the *b* group an *ab* mother produced an *ab* offspring. In the case of *d*, one of five offspring had the character, but this individual had a full sibling which was normal.

In the case of *b*, eight of eleven offspring had the character. This, however, is not very different from the proportion expected in a wild population at the temperatures obtaining (*see* Tables I and VIII). Also, of the four sets of siblings, while two agree in all possessing the character (5 offspring), the other two (4 offspring) each contain one normal individual. It may also be noticed that *a* turned up where *d* was expected, a *b* occurred in the *a* offspring, a *d* among the *b* offspring, and *f* among the *a* and *b* offspring.

Though this experiment is perhaps not conclusive, it cannot be said to offer any support to a simple inheritance theory.

VIABILITY OF VARIANT FLIES

During the conduct of the breeding experiment described above it was noticed that the variations being studied were in general more numerous in flies emerging in the laboratory than in the wild population. This observation led to the suggestion that flies possessing the variations might be less viable than normal flies, and hence might tend to be eliminated from the population. Table IV records the occurrences in male *G. swynnertoni* from three separate batches of puparia, and compares them with the occurrences in wild male *G. swynnertoni* collected a month later. Since the

mean life of male *G. swynnertoni* is believed to be about a month (Buxton, 1955 : 467), the members of each pair of such collections should be closely comparable. It is clear that the variations are not more common in tenerals, so that elimination of the kind postulated does not take place.

TABLE IV.—*Occurrence of variations in male* G. swynnertoni *emerging in the laboratory from wild pupae, compared with wild males collected in the following month*

		a	*b*	*c*	*d*	*e*	*f*	*g*	*h*	*j*	*k*	*l*	Examined
Tenerals .	December, 1953	94	48	4	11	36	14	0	0	4	2	0	1252
Wild .	January, 1954	94	62	8	10	48	13	0	0	9	1	0	1000
Tenerals .	September, 1954	9	7	0	3	8	1	0	0	3	0	0	285
Wild .	October, 1954	61	25	0	4	36	11	0	0	11	0	0	1000
Tenerals .	October, 1954	25	16	1	4	14	3	0	0	1	0	0	273
Wild .	November, 1954	132	103	24	25	74	24	0	0	15	6	2	1000

The reason for the anomaly which prompted the observations recorded in Table IV is that it was made at a time (November) when the incidence of variations is rising rapidly. At such times the incidence is necessarily greater in teneral flies than it is in older ones. A similar condition can be made out in Table IV by comparing the incidence in wild males in October 1954 with the incidence in tenerals emerging in the same month.

An unexpected finding from Table IV is that in four instances (*b* and *e* in December 1953 and *b* and *c* in October 1954) the incidence in tenerals is significantly less than it is in the wild population in the following month. This could be because of imperfect synchronisation ; the wild flies perhaps emerged not at exactly the same time as the tenerals.

OCCURRENCE OF THE VARIATIONS IN OTHER SPECIES OF *Glossina*

Most of the characters occur in other species of *Glossina*. In addition to the data presented in Table V, in *G. brevipalpis* Newstead the occurrence of *m* has been noted, and in *G. austeni* Newstead, of *b* and *d*. Comparing the three closely related forms *G. swynnertoni*, *G. morsitans morsitans* and *G. morsitans orientalis* we see that in the

TABLE V.—*Occurrences of venation variations in other species of* Glossina

	a	*b*	*c*	*d*	*e*	*f*	*g*	*h*	*j*	*k*	*l*	Number examined	Source
G. morsitans orientalis													
♂ .	2	0	0	0	0	0	0	0	0	0	0	60	Handeni T.T.
♀ .	0	0	1	1	0	0	1	0	0	0	0	60	Kingolwira.
♂ .	14	0	2	2	0	0	1	0	0	1	0	750	Kingolwira, Aug., 1953.
♂ .	12	0	1	1	0	0	0	0	0	0	2	490	Kingolwira, Dec., 1955.
G. morsitans morsitans													
♂ .	0	0	0	12	0	0	0	0	1	0	0	355	1944 release.
♂ .	0	0	0	4	0	0	0	0	0	0	0	385	1945 release.
♂ .	0	0	1	9	1	0	0	0	2	0	0	398	1946 release.
♂ .	0	0	1	3	0	0	0	0	0	0	0	107	Daga-Iloi, 1950.
♂ .	3	0	2	5	1	0	0	0	2	0	0	593	Mkweme, 1950–53.
♂ .	0	0	0	3	0	0	0	0	1	0	0	143	Butambara, May, 1953.
Total ♂ .	3	0	4	36	2	0	0	0	6	0	0	1981	

[*contd. overleaf*

TABLE V.—*Occurrences of venation variations in other species of* Glossina (contd.)

	a	*b*	*c*	*d*	*e*	*f*	*g*	*h*	*j*	*k*	*l*	Number examined	Source
♀	0	0	2	1	1	0	1	0	1	0	0	233	1946 release.
♀	0	0	3	0	0	0	0	0	2	0	0	123	Butambara, May, 1953.
G. pallidipes													
♂	0	1	0	0	0	0	0	0	0	0	0	126	Shinyanga, Aug.–Sept., 1946.
♂	0	2	0	0	0	0	0	0	0	0	0	314	Shinyanga, Apr.–Dec., 1956.
♂	2	0	0	1	0	0	0	0	1	0	0	709	Lambwe, May–July, 1953.
♀	0	1	0	0	1	0	0	0	0	0	0	258	Shinyanga, Apr.–Dec., 1956.

	a	*b*	*c*	*d*	*e*	*f*	*g*	*h*	*j*	*k*	*l*	*m*	Number examined	Source
G. palpalis fuscipes														
♂	0	0	0	0	0	0	0	0	0	1	0	0	46	Entebbe pupae, 1944–46.
♂	0	0	0	0	0	0	0	0	0	0	0	0	99	Kuja, 1946.
♂	0	2	1	0	0	0	1	0	0	2	0	2	385	Busoga, Jan.–July, 1955.
♂	2	0	0	0	0	0	0	0	0	0	0	0	259	Kuja, Oct., 1955, May, 1956.
♂	1	5	1	0	0	0	2	0	0	0	0	0	481	Rago, Waturi, Oct., 1955, May, 1956.
Total ♂	3	7	2	0	0	0	3	0	0	3	0	2	1270	
♀	0	1	0	0	0	0	0	0	0	1	0	0	9	Entebbe pupae, 1946.
♀	0	0	0	0	0	0	0	0	0	1	0	0	132	Kuja, 1946.
♀	0	0	0	0	0	0	0	0	0	1	0	0	294	Busoga, Jan.–July, 1955.
Total ♀	0	1	0	0	0	0	0	0	0	3	0	0	435	

Notes on the sources.—Handeni and Kingolwira are in the Eastern province of Tanganyika. The 1944–46 releases were releases in Shinyanga of *G. morsitans morsitans* from the Central Province of Tanganyika (Jackson, 1946 ; 1948). The Daga-Iloi flies were collected by Jackson (1955). Mkweme and Butambara are in the Kahama District of Tanganyika. Kuja, Lambwe, Waturi and Rago are in the South Nyanza District of Kenya. Busoga and Entebbe are on the northern shores of Lake Victoria, in Uganda.

first (in males) *e* or *b* is the most common character ; in the second *d* and in the third *a*. The pattern of occurrences is then a sub-specific character, although not one which would be of assistance in the identification of a single individual.

ASSOCIATION OF VARIATIONS

That some individuals will bear more than one variation is to be expected without the necessity of inferring linked inheritance because, as will be shown below, some, perhaps all, of the characters we are studying are more common in flies emerging from puparia which have experienced high temperatures. In nature some puparia doubtless experience temperatures above average and flies emerging from them would have enhanced chances of possessing both single and combined variations.

Records were not always kept of coincident variations, but data are available for four separate samples totalling 1974 male and 1865 female *G. swynnertoni*. Altogether 176 comparisons were made, and in eight cases simultaneous occurrences were " significantly " above expectation. As nine results would be expected to be significant at the 5 per cent. level in this number of trials, the only evidence for linkage lies in the fact that all these cases were positive, *i.e.* pairs of characters occurred more often than would be expected if they were in fact independent. The temperature effect, however, may well account for this.

Only one pair of characters, *b*–*c*, consistently occurred more often than expected and that only in males. The data are presented in Table VI.

TABLE VI.—*Occurrence of variations* b *and* c *in the same individual male* G. swynnertoni

	b	No *b*	Total
c . . .	13 (1·3)	5 (16·7)	18
No *c* . . .	131	1825	1956
Total .	144	1830	1974

The bracketed values are those expected if the characters occurred independently.

SYMMETRY

It was stated above that a variation may be observed in either wing, or in both. Table VII presents the positions of all the variations recorded in Table I. There are considerable differences between the various characters in respect of the symmetry of occurrence.

TABLE VII.—*Symmetry of variations observed in* 15,534 *male* G. swynnertoni *between July* 1953 *and November* 1954 (See *Table I*)

Variation	Left wing	Right wing	Both	Percentage symmetrical
a	243	235	125	21
b	147	179	40	11
c	18	14	12	27
d	42	37	3	4
e	236	271	60	11
f	72	59	5	4
g	.	.	.	.
h	.	.	.	.
j	34	39	9	11
k	5	8	0	0
l	4	2	0	0
m	1	0	0	0

If we consider the laboratory deposited pupae which were incubated at 29° C. (Table VIII), no less than 26 (53 per cent.) of males with *b* had it in both wings, a value significantly higher than the 11 per cent. recorded in Table VII. The numbers of other characters were too small for comparisons to be drawn. There is a suggestion that symmetry, as well as occurrences of *b*, may be promoted by high temperatures, but in the three hot months, November 1953, January and November 1954, the only months (Table I) in which occurrences of *b* exceeded 50 per 1000, the percentages symmetrical in respect of *b* were 11, 6 and 17.

THE EXPERIMENTAL INDUCTION OF VARIATIONS

First Experiment

In October 1956 puparia of *G. swynnertoni* were collected in Block 9 and divided into two equal batches. One was placed in an incubator at 30° C. and the other in a room kept at 22° C. The results appear in the third and fourth lines of Table II.

TABLE VIII.—*The occurrence of variations in the wings of tsetse emerging from puparia kept at two temperatures*

	a	*b*	*c*	*d*	*e*	*f*	*g*	*h*	*j*	*k*	Number in sample
					Males						
29° C.	16	49	9	4	9	9	0	0	2	2	90
20° C.	0	0	0	1	5	0	0	0	0	0	70
					Females						
29° C.	19	47	6	1	2	5	0	0	2	4	60
20° C.	0	0	0	0	2	0	0	0	0	0	60

The incidence of each variation is roughly the same in the two batches. The incidence is high and typical of the season and evidently unaffected by the treatment. It was concluded that if the seasonal change noted in Table I were really a temperature effect, the sensitive stage was earlier than the second half of pupal life, which was, on the average, the one treated in this experiment. Another experiment was therefore undertaken.

Second Experiment

Female *G. swynnertoni* were captured in Block 9 and maintained on sheep in individual 3 × 1-inch tubes in the breeding room. The temperature of this room was not controlled but was at this time (April 1958) about 25° C. Such females have usually mated naturally and males were not offered to them. Larvae are usually produced in the afternoon ; the resulting puparia were transferred next morning either to the incubator at 29° C. or to the cool room now at 20° C. Two days before the imagos were due to emerge the pupae were removed from the incubator at 29° C. and kept at room temperature (about 25° C.) in order to reduce mortality. The results of this experiment are given in Table VIII.

The differences observed are significant in the cases of *a*, *b*, *c* and *f*, in both sexes. With *d*, *e*, *j* and *k* the differences are not significant, although in all cases except *e* in females the incidence is higher in the group incubated at the higher temperature. That the difference in *e* in males is not significant is odd, as the seasonal effect in *e* in nature is well-marked (Table I) and in both years the November incidence is significantly higher than that of October.

DISCUSSION

Lower (1951), discussing the evolution of the venation of Diptera, remarks that " It is often the exceptional individual which provides the key to difficulties ". It is certainly tempting to suppose that an individual such as that shown in Plate I, fig. 4 provides a clue to the venation of an ancestor of *Glossina*. Such speculations, however, are perhaps inadmissable for the following reasons. It was mentioned above that the

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PLATE I

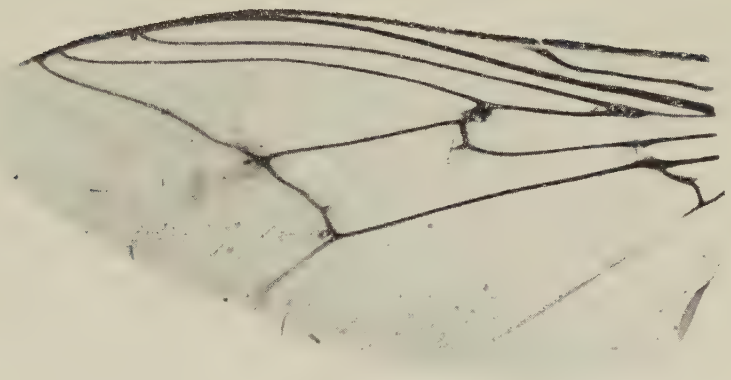
Glossina swynnertoni Austen

FIG. 1.—Left wing of a male from puparium incubated at 29° C., May, 1958. Abnormalities *a*, *b*, *c*, *f* and *j* are visible on one wing ; the *j*, however, is further from the edge of the wing than is typical.

FIG. 2.—Right wing of a male from puparium collected in Block 9, Shinyanga, on 2.vii.59 and incubated at room temperature. Abnormality *h*.

FIG. 3.—Left wing of a male collected in Block 9, Shinyanga, in July, 1953. Abnormality *e*.

FIG. 4.—Both wings of a male emerged from puparium collected in Block 9, Shinyanga, on 18.vi.59 and incubated at room temperature. Left wing shows abnormalities *b* and *c* ; right wing has *b* and *c* joined in the very rare condition which divides the hatchet cell in two ; in addition, the right wing has *e*.



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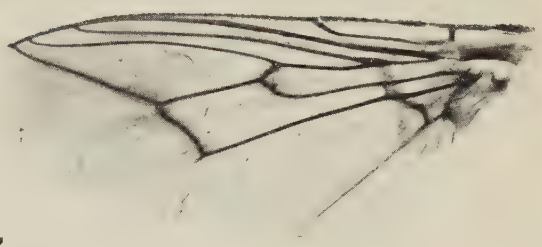

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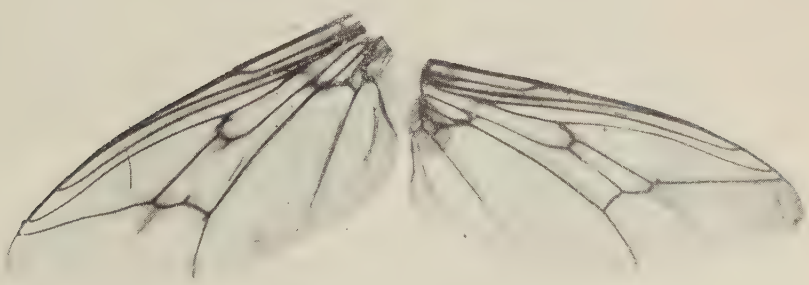

4

The wing venation of *Glossina swynnertoni* Austen.

J. P. Glasgow

pattern of occurrence of the variations is characteristic of a species. If the pattern is to be allowed ancestral significance, then we shall be led to suppose that the ancestor of *G. swynnertoni* Austen usually or always possessed *b* and *e* while the ancestor of *G. morsitans morsitans* Westwood had *d*. That is to say, the immediate ancestors of these two species differed more than the modern species. This conclusion seems unacceptable in view of the remarkable uniformity of the venation of the twenty-two modern and four fossil species of the genus (Buxton, 1955 ; Hegh, 1929).

Burtt (1946) found that tsetse derived from pupae incubated at high temperatures transmitted trypanosomes more readily. It is therefore possible that wing variations may be found to coincide with infectibility. It may also be possible so to calibrate the temperature-wing variation effect that information may be inferred about the temperature of natural breeding sites.

Summary

1. Eleven variations in the wing venation of *Glossina* species are described. Nine are supernumerary stub veins, and two are gaps in the normal venation.

2. Seasonal changes occur in the incidence of these variations ; they are most common shortly after the hottest months.

3. The incidence of the variations differs between the sexes, and between species.

4. An attempt to demonstrate that the variations are inherited as Mendelian recessives was unsuccessful.

5. No difference in viability has been found in flies with and without the variations. Observed differences in incidence between young and old flies are ascribed to the seasonal changes.

6. There is slight evidence that some of the variations may be associated with each other.

7. The variations may occur in both wings, but more usually are found in only one. The incidence of symmetry differs between variations, and also within any one variation at different times.

8. Some of the variations may be induced experimentally by subjecting puparia to high temperatures. This effect was demonstrated in laboratory bred puparia which were incubated from the day after birth, but not with wild puparia which had on the average lived half their lives at the time of collection.

9. Reasons are given for not attaching phylogenetic significance to the variations ; they may, however, have epidemiological and ecological meaning.

Acknowledgments

I am indebted to the late Dr. C. H. N. Jackson and to Mr. Yahya Mohamed for examining the monthly samples during my absence at the Uganda out-station in 1954, to Dr. E. Bursell for supervising the breeding of puparia for the induction experiment, and to Mr. C. J. Webb for taking the photographs.

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VARIATIONS IN THE VENATION OF *GLOSSINA MORSITANS ORIENTALIS* VANDERPLANK (DIPTERA: MUSCIDAE)

By J. R. Welch

(*East African Trypanosomiasis Research Organization, Tororo, Uganda*)

[Communicated by Dr. J. P. Glasgow]

Further to the work of Glasgow (*antea* pp. 49–57) on variations in the venation of *Glossina*, a series of observations was made on the venation of 5596 pairs of wings of *Glossina morsitans orientalis* Vanderplank, comprising 5190 males and 406 females. The specimens examined were collected between March 1957 and February 1958, from the Kingolwira and Kitulangalo areas, within the large loop of the Ngerengere River 15–20 miles northeast of Morogoro, Tanganyika Territory.

The range of variations was less than that observed by Glasgow in *G. swynnertoni* Austen, the only ones seen being *a*, *c*, *d*, *e*, *l* and an additional one, which has been designated *n* and is shown in figure 1. In addition Glasgow (p. 53) recorded two examples of variation *g* in specimens from Kingolwira. The occurrences of variations in males are shown in Table I.

Although there was a slightly higher proportion of variant flies after periods of hot weather, there was no significant correlation between the percentages of male flies with aberrant wings and the mean temperatures of the same month, nor of either

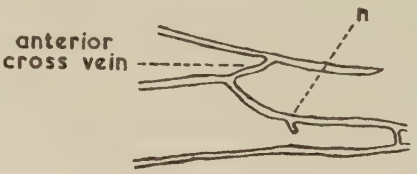

Fig. 1.—Variation *n* in the wing veins of *Glossina morsitans orientalis*.

Table I.—*Occurrences of variations in the wing veins of male* Glossina morsitans orientalis

1957	*a*	*c*	*d*	*e*	*l*	*n*	Total	Number examined	%	Mean temp. (°C.)	1½″ soil temp. (°C.). Mean 2 p.m.
January	.	.	.	.	.	.	.	.	.	26·2	36·1
February	.	.	.	.	.	.	.	.	.	25·9	40·0
March	7	0	0	0	0	0	7	382	1·83	26·4	37·2
April	12	0	2	0	0	1	15	553	2·71	25·5	34·4
May	20	1	4	0	0	0	25	420	5·95	24·3	33·3
June	23	0	1	0	0	0	24	420	5·71	22·6	36·7
July	11	1	2	0	0	1	15	469	3·20	22·5	37·2
August	6	1	2	0	0	0	9	385	2·34	23·3	40·6
September	10	1	0	1	0	0	12	419	2·86	24·3	40·6
October	.	.	.	.	.	.	.	.	.	25·8	41·1
November	17	0	2	0	0	0	19	520	3·65	25·1	35·6
December	13	0	1	0	0	0	14	531	2·64	26·4	39·4
1958											
January	26	0	2	1	1	0	30	560	5·36	27·9	45·0
February	25	0	1	0	0	0	26	531	4·90	.	.

of the two previous months, nor was there any correlation with mean monthly 2 p.m. 1½-inch soil temperatures, similarly tested.

In Table II a comparison has been made between the occurrences of variations in males and females over the whole year.

TABLE II.—*Occurrences of variations in males and females*

	Numbers examined	*a*	*c*	*d*	*e*	*l*	*n*	Total	%
Males	5190	170	4	17	2	1	2	196	3·78
Females	406	7	10	5	1	0	0	23	5·67

Proportionately more variations occurred in female than in male flies, but the differences in the totals were not significant when all the variations were considered together ($\chi^2 = 2{\cdot}97$, $P > 0{\cdot}05$), or when the variations of *a*, *d* and *e* were considered separately. There were significantly more variations of type *c* in females than in males ($\chi^2 = 30{\cdot}25$ $P < 0{\cdot}001$) and *l* and *n* were seen only in males, but their numbers were too few for any statistical significance to be shown. The significant difference in the occurrences of *c* is, however, indicative of some connection with sex.

In Table III a comparison has been made between the occurrences of variations observed in male *G. morsitans orientalis* and those recorded by Glasgow in *G. morsitans morsitans* Westwood and *G. swynnertoni*.

TABLE III.—*A comparison of the occurrences of variations in male* Glossina swynnertoni, G. morsitans orientalis *and* G. morsitans morsitans

Variation	Numbers of occurrences: *G. swynnertoni*	*G. m. orientalis*	*G. m. morsitans*
a	603	170	3
	Significantly more in *G. swynnertoni* than in *G. m. orientalis* $P > 0{\cdot}02$ but $< 0{\cdot}05$		
b	366	0	0
c	44	4	4
	Significantly more in *G. swynnertoni* than in *G. m. orientalis* $P > 0{\cdot}01$ but $< 0{\cdot}02$		
d	82	17	36
		Significantly more in *G. m. morsitans* than in *G. m. orientalis* $P < 0{\cdot}01$	
e	567	2	2
	Significantly more in *G. swynnertoni* than in *G. m. orientalis* $P < 0{\cdot}001$		
f	136	0	0
g	0	1*	0
h	1	0	0
j	82	0	6
k	13	0	0
l	6	1	0
n	0	2	0
Total examined	15,534	5,190	1,981

* From separate sample of 750; none found in three samples of 5,190, 60 and 490.

The table shows considerable differences in the occurrences of variations, some of these differences being statistically significant. The numbers examined were insufficient for definite conclusions to be drawn, but the results obtained do help to confirm the classification. At present *G. morsitans morsitans* and *G. morsitans orientalis* are classified as sub-species of *G. morsitans*, with *G. swynnertoni* as a separate species, but there is some doubt as to its specific status, and it may eventually come to be regarded as a third sub-species of *G. morsitans*. The differences in incidence of variations in the venation (Table III), while not sufficient in themselves as criteria of classification, do offer confirmation of the concept that there are three valid taxonomic units.

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Book Notice

The Plant Galls of Norway. By D. Leatherdale. *Univ. Bergen Arb. naturv. R.* **8**: 1–56, text illust. 1959.

This is a preliminary catalogue of the plant galls of Norway based on the collection in the Zoological Museum, University of Bergen.

Altogether 273 galls on 122 host plants are recorded, including galls caused by both plants and animals. The arrangement is botanical and under each heading are given the scientific and Norwegian common name for each plant, the scientific name of the gall-causer, references to literature, location, date, collector and the Zoological Museum's Collection number. As many references to Norwegian records as possible have been included.

In addition to the main catalogue there is also an index to plant families and genera, a classified index of gall causers and a bibliography.

ON THE USE OF THE TERMS " LARVA " AND " NYMPH" IN ENTOMOLOGY

By Chang-Whan Kim

(*From the Department of Zoology, University of Cambridge*[1])

Berlese (1913) classified insect larvae on the basis of the resemblances which they show to three phases: protopod, polypod and oligopod. He considered that the larval stage of the Endopterygota is homologous with the last part of the embryonic development of the Exopterygota, whilst the nymphal stage of the latter corresponds to the pupal stage of the former.

Imms (1937) developed Berlese's theory, recognising his three phases and adding a fourth, the apodous type, derived mainly from the polypodous type. He considered that Dipterous larvae are probably to be regarded as highly specialized derivatives of the oligopod type, for a clearly defined polypod phase has become obliterated from all stages in the ontogeny of most flies.

Pérez (1910) and Handlirsch (1927) supposed that the pupal stage arose by the concentration of the changes from nymph to adult into the last instar. On this view the pupa would correspond to the last nymphal instar (Southwood *et al.*, 1958). Hinton (1948), however, revived and modified Poyarkoff's theory (1914) which supposed that the pupa of the Endopterygota represents the first of two adult instars.

As described by Kim (1959), the first segment of the caterpillar's leg in *Pieris* forms the coxa of the adult leg, the thickened part on the inner side at the base of the second segment grows to form the trochanter, and, as was pointed out by Gonin (1894), the femur and tibia arise from the out-growth of the femoro-tibial bud. During the prepupal period a septum appears in this out-growth, and after pupation the femur and tibia are completely separated. The third and fourth segments of the caterpillar's leg give rise to the tarsus.

The so-called imaginal bud described by Bodenstein (1935, 1937), which arises during embryonic development, is not a bud that remains within the body during larval life like the wing bud; it forms a functioning part of the larval leg. The leg remains unchanged during larval life apart from some increase in size, and finally develops into the adult leg during the pupal stage. One can, therefore, regard the larval leg *as a whole* as an " imaginal bud " which functions as a limb.

Roonwal (1937) has described the development of the leg in *Locusta*. According to his observations the leg buds appear in the embryo at 52 hours; at 70 hours they resemble the leg buds of the dipteran prepupa. The newly segmented leg buds at 100 hours resemble the legs of a caterpillar in form and the embryonic legs shortly after blastokinesis resemble the prepupal legs in *Pieris* at the time when the femur and tibia separate. Roonwal writes " in about the 120-hours stage, a minute invagination is formed on the ventral surface of the femora of the pro- and mesothorax but not of the metathorax. These invaginations disappear shortly after blastokinesis ". This invagination may be the process dividing the femur and tibia into two parts, as in *Pieris*.

If the legs of the caterpillar had no function at all, like embryonic legs in Exopterygota, one would regard them as imaginal buds comparable with the wing bud of Endopterygota or Exopterygota. But since they are fully functional, they are not commonly thought of as imaginal buds.

In Exopterygota the development from leg rudiment to adult leg proceeds without a break. In Lepidoptera it is interrupted at an intermediate stage (the larval stage) and the adult legs are completed during the pupal stage by a process of development

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which closely resembles that in the exopterygote thoracic leg. In the Diptera the development of the leg is arrested at a very early stage.

Weismann (1864) made the following observations on the development of legs in Muscidae. The rudiments of appendages appear first, and later the five tarsal segments, at the end of the tibia ; the proximal part of the tibia, which he termed " Femorocoxalstueck " (which is, in fact, the femoro-tibial bud of Gonin), grows directly outward, as a short oblique out-growth, free from the thorax. In the early stage it has a simple spacious lumen ; later it is split in half by a dividing-wall. In this way two parts of the limb are built from the " Femorocoxalstueck " just as was described in *Pieris* (Kim, 1959). Weismann, however, thought that the coxa and

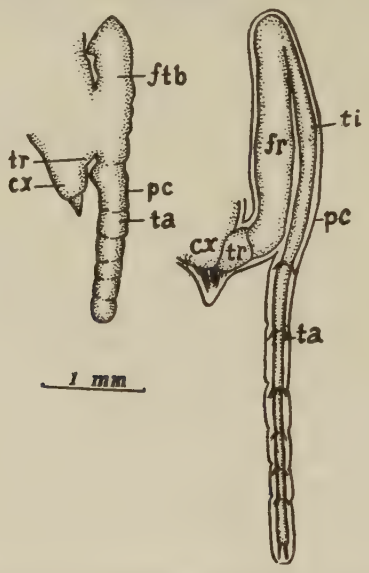

Fig. 1.—Two stages of the developing mesothoracic leg in the pupa of *Calliphora erythrocephala* Meigen. *Left*, fourth day stage ; *right*, seventh day stage. (*cx*, coxa ; *tr*, trochanter ; *ftb*, femoro-tibial bud ; *ta*, tarsus ; *fr*, femur ; *ti*, tibia ; *pc*, pupal cuticle.)

trochanter were derived from the inner part of the process, the femur partly from this and partly from its upper part, and the tibia from the outer part.

In *Calliphora* the segmented leg appears on the second day after pupation. On about the third day the femoro-tibial bud grows out as Weismann described. The bud becomes larger and larger and is clearly divided into two parts, femur and tibia, on about the seventh day after pupation (fig. 1). The coxa and trochanter are built at the proximal part of the bud.

These facts suggest that development of the adult thoracic leg in insects of all kinds proceeds by the same sequence : leg rudiment, segmented leg, femoro-tibial bud which is divided into femur and tibia, and completed adult leg. The Exopterygota do this without a break during the embryonic stage, Diptera only during the pupal stage and in Lepidoptera the development is interrupted at the segmented leg stage and then completed during the pupal stage.

This evidence supports the Berlese theory on some counts, but adherents to that theory usually treat the larval stages of all Endopterygota as identical phases. The nymphal stage in Exopterygota corresponds to the pupal stage in Lepidoptera, but the pupal stages in Diptera should be considered as equivalent to the larval plus pupal stages in Lepidoptera, so far as the thoracic leg formation is concerned (*see* fig. 2). Observations in *Pieris* show that the epidermis of the pupa differentiates to form adult characters, for example scales and hairs, at the middle period of the pupal

stage. Such changes perhaps correspond to the changes from nymph to adult in Exopterygota.

Some of the leaf-mining Lepidoptera lack thoracic legs in the first but not in the second and following instars (Hinton, 1955). In this case the larva may hatch from the egg at a little earlier stage than most other caterpillars. In Diptera, hatching occurs at an early point in embryonic development, and consequently the first stages of their larvae are the most immature of the forms considered ; in Lepidoptera hatching takes place at a slightly later stage of development, and in the Exopterygota at a still later stage with the nymph representing the most advanced active immature phase (fig. 2). Dipterous larvae are probably to be regarded as highly specialized

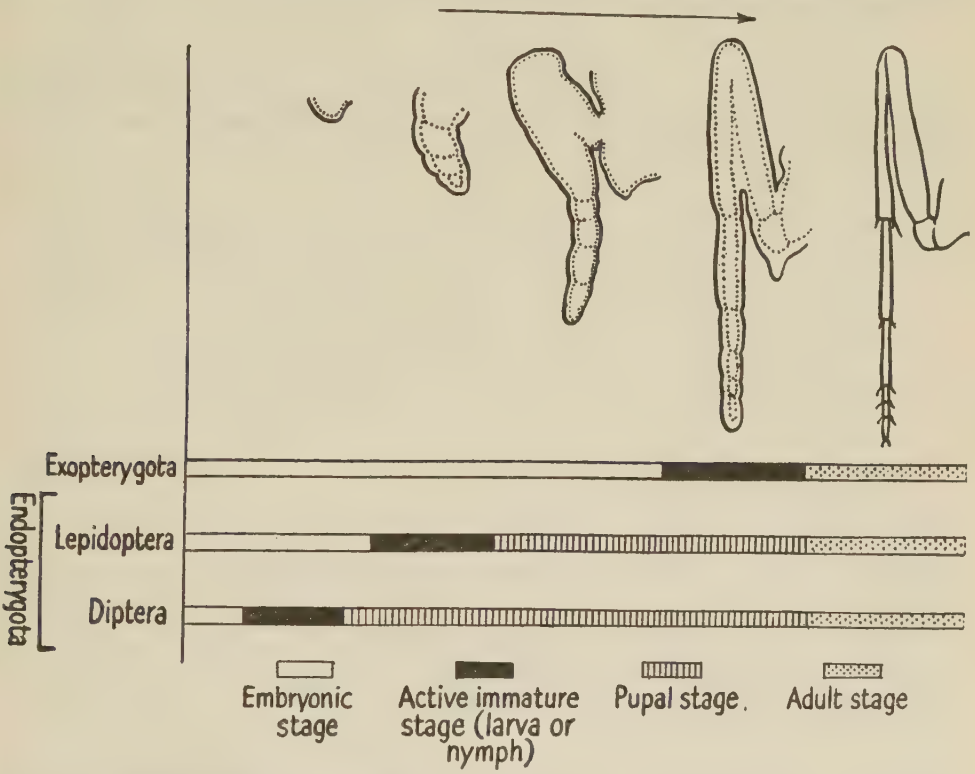

Fig. 2.—Diagram showing various phases in Exopterygota and two main groups of Endopterygota on the basis of the thoracic leg development.

(Note.—Corresponding phases in thoracic leg development are shown in the vertical plane.)

examples of very early hatching and not as derivatives of an oligopod type, as described by Imms. The active immature phases of Diptera and Lepidoptera are therefore different, although both are called larvae. The active immature phase in Lepidoptera, the caterpillar, is always regarded as a larva, although, so far as thoracic leg development is concerned, it corresponds to the early stage of the pupa in Diptera. But there is much disagreement about calling the nymph, which corresponds to the early pupal stage in Lepidoptera, a larva, although it, too, is the active immature stage.

In that they are all active immature stages, the maggot, caterpillar and nymph may be looked on as larvae. However, this present work shows that thoracic leg development has reached a different stage in the maggot, caterpillar and nymph. Thus, though functionally the same, these represent different stages in development.

It is therefore suggested that the differences between the larvae of Diptera and Lepidoptera, and the differences between the larva and nymph, depend upon the differences in the developmental stage at which they hatch, and are the result of adaptation and evolution.

Presumably the same thing happens in wing development, giving rise to the division of winged insects into Endopterygota and Exopterygota.

The Poyarkoff-Hinton theory which regards the nymph as the larva, and the Berlese-Imms theory in which the nymphal stage corresponds to the pupal stage in Endopterygota, both show part of the truth. The nymph in Exopterygota may be regarded as an active immature phase (a larva) which corresponds to the middle stage of the Dipterous pupa or the early stage of the Lepidopterous pupa.

Acknowledgments

This work was carried out in Cambridge while holding a British Council Scholarship. I should like to thank Professor V. B. Wigglesworth for his assistance in preparing the manuscript.

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THE GREEN MUSCARDINE DISEASE OF INSECTS, WITH SPECIAL REFERENCE TO AN EPIDEMIC IN A SWARM OF LOCUSTS IN ERITREA

By Frances L. Balfour-Browne
(*British Museum (Natural History)*)

[Communicated by Dr. T. H. C. Taylor]

Introduction

A consignment of locusts from a swarm in Eritrea was received from Dr. T. H. C. Taylor of the Anti-Locust Research Centre. The insects were heavily infected with a fungus which proved to be *Metarrhizium anisopliae*, the causal agent of the Green Muscardine disease. This fungus, which parasitises a large variety of insects in both temperate and tropical countries, has been extensively used in attempts at biological control of insect pests. As the literature referring to the disease is widely scattered it was decided, in addition to reporting the present occurrence, to summarise the more salient records and features already known and to include a reasonably full bibliography to compensate for the briefness of the exposition.

General Report on the Locust Swarm

The consignment in question concerns the desert locust, *Schistocerca gregaria* (Forskål), and was recorded at Kilometre 75 on the Asmara-Massawa Road in Eritrea, mainly on 25th February, 1959.

I am indebted to Dr. Taylor for the reports, quoted verbatim below, received from Messrs D. Watson Cook and E. G. Wallace, who made the observations in the field.

" The mature swarm arrived from the North East and began to settle in the hills to the East of Ailet plain (elevation approximately 1,200 ft.) at about 17.00 hours on 20th February. It was described by the reporting officer, Mr. D. Watson Cook, as being 5 × 1 miles in size, thin density and flying low. The swarm settled mainly on trees and bushes of *Acacia* sp. and *Salvadora* sp. situated on the steep rocky sides of a wadi. The sky was overcast and the air rather humid, which were the conditions prevailing in this locality since 14th February. During the next three days copulating and laying occurred, egg pods being deposited in the small patches of sand between rocks. Fine, steady rain fell in the area on 22nd, 23rd and 25th February and overcast conditions continued until approximately mid-day on the 27th, when the sun appeared for about four hours. During this time, the swarm departed from the site in which it had roosted for the last six days and its size was much reduced. It settled again in the Ailet plain two miles to the west of the former site, having left many dead in its track.

" On 25th February, during a close inspection of the roosting swarm, it was noticed that many locusts were dead and dying in a characteristic position, with head up, front legs embracing part of a tree and hind legs free. A fungus was observed on the outside of the abdomen of those locusts affected and, in some, the inside of the abdomen and neck also contained the fungus.

"It was decided to count the number of dead locusts in and under each tree in a few sample areas, but owing to the torpid condition of the whole swarm this could not be carried out until improved weather conditions had induced flight. The counts were made on 27th February and 2nd March during and after departure of the remnants of the swarm. Three areas, each of 100 yards square and containing 47, 29 and 40 bushes respectively, gave the following counts of dead locusts :

"*First Area—27th February* (47 bushes): 19, 61, 22, 12, 17, 12, 38, 8, 87, 27, 30, 7, 18, 20, 29, 52, 15, 46, 48, 28, 40, 120, 145, 66, 117, 42, 67, 25, 32, 35, 140, 36, 200, 56, 38, 15, 74, 41, 8, 114, 12, 8, 48, 21, 12, 17, 63.

"*Second Area—27th February* (29 bushes): 35, 27, 49, 33, 65, 12, 78, 22, 91, 28, 43, 52, 29, 33, 101, 71, 35, 77, 29, 51, 78, 10, 110, 55, 3, 41, 91, 44, 103.

"*Third Area—2nd March* (40 bushes): 40, 97, 63, 55, 83, 24, 20, 31, 77, 56, 29, 12, 22, 95, 8, 33, 24, 21, 13, 44, 85, 39, 24, 41, 50, 12, 85, 33, 91, 80, 43, 41, 11, 99, 71, 73, 21, 45, 70, 22."

About a fortnight later the following additional report was received:

"The swarm from which the diseased locusts were taken (reference Km. 75 Asmara-Massawa road 25.ii.59) is believed to have been largely destroyed by the fungus. Only a few scattered locusts were seen leaving the area and at the last roosting site many dead were found, some of which were heavily diseased, with most of the head and thorax covered with the thick white fungus. The swarm laid between 21st and 23rd February and hatching occurred on the 15th March."

History of the Fungus and of Experimental Work

The fungus species responsible for this epidemic was first recorded by Metschnikoff in 1879 as *Entomophthora anisopliae* on the cockchafer of wheat, *Anisoplia austriaca* Herbst, in Russia. Sorokin in the same year proposed the generic name *Metarrhizium* for it. In the following decade or so the fungus was redescribed under different names as indicated in the synonymy here given:

Entomophthora anisopliae Metschnikoff, 1879
Metarrhizium anisopliae (Metsch.) Sorokin, 1879
Isaria destructor Metschnikoff, 1880
Oospora destructor (Metsch.) Delacroix, 1893
Penicillium anisopliae (Metsch.) Vuillemin, 1904
Penicillium cicadinum von Hoehnel, 1909
Septocylindrium suspectum Massee, 1910

As the fungus is not a species of *Entomophthora* (Phycomycetes) but belongs to the Hyphomycetous group of the Fungi Imperfecti, it cannot be left where it was originally placed; and as it cannot satisfactorily be placed in either *Isaria*, *Oospora* or *Penicillium* it has for the last 30 years or so generally been segregated under Sorokin's genus *Metarrhizium*, of which it is the type species, i.e. *M. anisopliae* (Metsch.) Sorokin.

The fact that it is able to develop on many different species of insects is shown by the accompanying table (Table I) of the more outstanding records; in addition, it has been artificially transmitted to many other insects in the course of experimental work (Table II), especially in connection with its possible value as an agent for the biological control of noxious insects.

Various methods have been utilised in introducing the fungus into test insects. Vast (1904) successfully parasitised beetle larvae by dipping them in a water suspension of the fungal spores or by painting them with a brush to which spores were attached. Groenewege (1916) transferred the disease from *Adoretus* (*Anomalus*) *compressus* to *Oryctes rhinoceros* and *Helotrichia helleri* by breeding them on soil heavily contaminated with spores. Friederichs (1920) in Samoa, Madagascar, France, Switzerland and elsewhere recorded the disease occurring naturally on a great many insects and, in his experiments, infected many others. He transmitted the disease from species to species first by feeding them a paste of tapioca and sugar mixed with fungal spores, and, in his later experiments, by dusting, painting or spraying with spore powder or by shaking them up in containers provided with a culture of the fungus. Glaser (1926), working with silk worms, found that painting the larvae with spores gave 100 per cent. mortality whereas feeding them with the fungus was

TABLE I.—*The host range of the Green Muscardine fungus*

Order	Insect	Locality	Authority
ORTHOPTERA .	*Anacridium aegyptium* (L.)	Egypt	Nattrass, 1932.
	Crickets	Ceylon	Petch, B.M. Herb., 1917.
	Cyrtacanthacris nigricornis Burm.	Java	Rutgers, 1916.
	Nomadacris septemfasciata Serville	N. Rhodesia	Lewin, 1936.
	Scapteriscus borellii Giglio-Tos	Argentine	Marchionatto, 1944.
	Schistocerca gregaria (Förskal)	Eritrea	This paper.
	Schistocerca paranensis Burm.	Argentine	Marchionatto, 1944.
DERMAPTERA .	Earwigs	Portland, Oregon	Barss and Stearns, 1925.
	,,	Ceylon	Petch, B.M. Herb., 1927.
HEMIPTERA .	*Cicada* sp.	Tjibodas, Java	von Hoehnel, 1909.
	Cicada viridis Stål	Mauritius	Petch, B.M. Herb., 1936 and 1938.
	Magicicada septendecim (L.)	Maryland, U.S.A.	Katsura and Johnson, 1937.
	,, ,, ,,	Maryland, U.S.A.	Susman, 1951.
	Perkinsiella vastatrix Breddin	Philippines	Petch, B.M. Herb., 1932.
	Phromnia marginella Stål	Ceylon	Petch, B.M. Herb., 1909.
	Pseudococcus sp.	Mauritius	Petch, B.M. Herb., 1941.
	Tomaspis postica Walk.	Trinidad	Rorer, 1910.
LEPIDOPTERA .	*Cirphis unipuncta* (Haw.)	Argentine	Marchionatto, 1944.
	Galleria mellonella (L).	France	Boczkowska, 1935.
	Pyrausta nubilalis (Hüb.)	Sweden and Jugoslavia	Wallengren, 1931.
	Pyrilla sp.	India	Kamat *et al.*, 1952.
	,, ,,	India	Mishra, 1953.
	Stenodontes sp.	Samoa	Friedrichs, 1920.
COLEOPTERA .	*Adoretus compressus* Web.	Java	Groenewege, 1916.
	A. mauritianus Ohs.	Mauritius	Petch, B.M. Herb., 1937.
	A. umbrosus F.	Hawaii	Speare, 1912.
	Agriotes mancus Say	Ithaca, U.S.A.	Pettit, 1895.
	Anisoplia austriaca Hrbst.	S. Russia	Metschnikoff, 1879.
	Anomala aenae (Deg.)	Poland	Siemaszko, 1937.
	A. orientalis Waterh.	Hawaii	Muir and Groenewege, 1916.
	Anomala sp.	Hawaii	Speare, 1912.
	Balaninus caryae Horn	Alabama, U.S.A.	Swingle, 1935.
	Cerambycid larvae	Madagascar	Friederichs, 1920.
	Cetonia sp.	? France	Vuillemin, 1904
	Cleonus punctiventris Germ.	S. Russia	Metschnikoff, 1879.
	,, ,, ,,	Ukraine	Wize, 1929.
	Cotinis texana Casey, larvae	U.S.A.	Phillips and Fox, 1924.
	Diaprepes abbreviatus L., larvae	Barbados	*Agric. News*, 1914.
	Diloboderus abderus Sturm	Argentine	Marchionatto, 1944.
	Elaterid larvae	U.S.A.	Hyslop, 1915.
	,, ,,	Madagascar	Friederichs, 1920.
	Encya condensata (Gerst.)	Madagascar	Friederichs, 1920.
	Ergates faber L.	S. France	Friederichs, 1920.
	Geotrogus deserticola Blanch.	Algeria and Morocco	Moutia, 1940.
	Lamellicorn larvae	Siam and Malaya	Friederichs, 1920.
	Lamprophorus sp.	Ceylon	Petch, 1931.
	Lepidioderma albohirtum Wat.	Queensland, Australia	Jarvis, 1916.
	Lethrus cephalotes Pall.	S. Russia	Metschnikoff, 1879, 1880.
	Leucopholis rorida F., larvae	Java	Groenewege, 1916.
	Melolontha melolontha (L.)	Poland	Siemaszko, 1937.
	Melolontha sp.	France	Delacroix, 1893.
	Oryctes radama Coq.	Madagascar	Friederichs, 1920.

[*contd. overleaf*

TABLE I.—*The host range of the Green Muscardine fungus* (contd.)

Order	Insect	Locality	Authority
COLEOPTERA (*contd.*)	*O. rhinoceros* L.	Java	Groenewege, 1916.
	,, ,, ,,	Philippines	Friederichs, 1920.
	,, ,, ,,	Samoa	Friederichs, 1920.
	,, ,, ,,	Ceylon	Petch, 1931.
	Phytalus smithi Arrow	Madagascar	Petch, B.M. Herb., 1935.
	Rhabdocnemis obscura Boisd.	Hawaii	Spear, 1912.
	Rhagium inquisitor (L.) (all stages)	S. France	Friederichs, 1920.
	R. inquisitor larvae	Berne, Switzerland	Friederichs, 1920.
	Rhynchophorus ferrugineus Ol.	Ceylon	Petch, B.M. Herb., 1922.
	Sternotomis maculata Hintz.	Madagascar	Friederichs, 1920.
HYMENOPTERA	Black ants	Ceylon	Petch, B.M. Herb., 1923.
	Campsomeris quadrifasciata	Philippines	Petch, B.M. Herb., 1935.

not destructive, as Metschnikoff and others also found. Boczkowska (1935), studying the immunity of larvae of *Galleria mellonella* (L.) to the *Metarrhizium* disease, found that injections of spore emulsions were more rapidly fatal than external inoculations, and the latter method was more effective than dusting with spore powder. Le Moult (1923) relates how he became acquainted with the Russian professor Krassilstchik (1888), who had built an experimental factory at Smela (Kiev) for the artificial production of the *Metarrhizium* fungus, parasitic on *Cleonus punctiventris* Germ., a pest of sugar beet. It is said that in four months he produced 55 kg. of pure spore powder on maize beerwort. With this, epizootics were initiated in small areas, destroying 55–80 per cent. of the insects in 10–15 days.

However, results and experience over the past 50 years suggest that, although laboratory and cage experiments are frequently highly successful, and whereas field trials may also give reasonably positive results, they are disappointing in that they fail to result in widespread control or to disseminate the disease to (locally) epizootic proportions (Petch, 1925; Simmonds, 1941). Other workers, however, are more optimistic. The Swedes Notini, Mathlein and Lihnell (1944) consider that the outlook for the practical application of the Green Muscardine for the extermination of insects is favourable. They obtained 40 per cent. mortality in preliminary tests against the grain moth *Tinea secalella* Zacher, by spraying warehouse walls with water and spores. Wallengren (1931), in Sweden, considered that his field experiments gave good results. He protected maize plants from infestation by *Pyrausta nubilalis* Hübn. by dusting them with spores of the fungus, either in the pure state or mixed with potato flour. Hergula in Jugoslavia confirmed his findings. Again reports from the Burma Department of Agriculture, 1941–1943, claimed that inoculating trap-pits with the *Metarrhizium* reduced the number of living grubs of the rhinoceros beetle of coconut by 15 per cent in one locality and by 70 per cent. in another. Earlier reports (1924) from the same district gave 100 per cent. infection.

It has been suggested that the different results obtained when attempting to infect insects with spores in soil and compost traps depend on a critical moisture content. Thus Dutky (*see* Gardner, 1957), working on Japanese beetle larvae, was able to obtain either no infection or 100 per cent infection by varying the moisture content of the soil and spore mixture. With too low a moisture level the spores adhere to the soil particles and the insect can move through the medium without infection, whereas with a high moisture content it will become plastered with the mixture and infection will ensue.

Spontaneous epizootics in nature support these findings as they always appear to synchronise with warm humid weather and with conditions generally favourable to fungal development, and relatively unsuitable for a healthy insect population. Rutgers (1916), in Java, correlated a high January rainfall with high incidence of Green Muscardine in the grasshopper, *Cyrtacanthacris nigricornis* Burm., and by mid-

TABLE II.—*Some of the insects artificially infected with the Green Muscardine fungus*

Order	Insect	Locality	Authority
ORTHOPTERA .	*Barbitistes pulchripennis* Costa	S. France	Friederichs, 1920.
	Periplaneta australasiae F.	Madagascar	Friederichs, 1920.
	Phasgonura viridissima L.	S. France	Friederichs, 1920.
HEMIPTERA .	*Acanthia lectularia* (L.)	S. France	Friederichs, 1920.
	Tomaspis postica Walk.	Trinidad	Williams, 1921.
LEPIDOPTERA .	*Agrotis segetum* (D. and S.)	Sweden	Notini *et al.*, 1944.
	A. nigricans Schiff.	Sweden	Notini *et al.*, 1944.
	A. tritici (L.)	Sweden	Notini *et al.*, 1944.
	Argyresthia conjugella Zell.	Sweden	Notini *et al.*, 1944.
	Barathra brassicae (L.)	Sweden	Notini *et al.*, 1944.
	Blastodacna putripenella Zell.	Sweden	Notini *et al.*, 1944.
	Bombyx mori Hüb.	France	Delacroix, 1893.
	Cerapteryx graminis (L.)	Sweden	Notini *et al.*, 1944.
	Cnethocampa pityocampa (F.)	S. France	Friederichs, 1920.
	Cossus cossus (L.)	Sweden	Notini *et al.*, 1944.
	,, ,, ,,	Germany	Friederichs, 1944.
	Dasychira pudibunda (L.)	Sweden	Notini *et al.*, 1944.
	Ephestia kühniella Zeller	Sweden	Notini *et al.*, 1944.
	Galleria mellonella(L.)	Sweden	Notini *et al.*, 1944.
	Heliothis dipsaceus (L.)	S. Russia	Metschnikoff, 1880.
	Hoffmanophila pseudospretella Staint.	S. Russia	Metschnikoff, 1880.
	Lozopera sp.	Berne, Switzerland	Friederichs, 1920.
	Lycaena sp.	Madagascar	Friederichs, 1920.
	Lymantria dispar (L.)	Sweden	Notini *et al.*, 1944.
	Polia oleracea L.	Sweden	Notini *et al.*, 1944.
	P. pisi L.	Sweden	Notini *et al.*, 1944.
	Rhyacia pronubia L.	Sweden	Notini *et al.*, 1944.
	Saturnia pyri (D. and S.)	S. France	Friederichs, 1920.
	Sphinx pinastri (L.)	Sweden	Notini *et al.*, 1944.
	Tinea secalella Zacher	Sweden	Notini *et al.*, 1944.
	Tortrix paleana (Hüb.)	Sweden	Notini *et al.*, 1944.
	T. viridana (L.)	Sweden	Notini *et al.*, 1944.
COLEOPTERA .	*Chalcophora mariana* L.	S. France	Friederichs, 1920.
	Holotrichia helleri Brenske	Java	Groenewege, 1916.
	Lepidiota rothei Blackb.	Queensland	Jarvis, 1916.
	Lethrus cephalotes Pall.	S. Russia	Metschnikoff, 1880.
	Leucopholis rorida F.	Batavia	Rutgers, 1916.
	Melolontha hippocastani F.	Sweden	Notini *et al.*, 1944.
	M. vulgaris F.	Switzerland	Friederichs, 1920.
	Oryctes rhinoceros L.	Ceylon	Bryce, 1915 and frequently since.
	Otiorrhynchus sulcatus (F.)	Switzerland	Friederichs, 1920.
	Rhagium bifasciatum F.	Berne, Switzerland	Friederichs, 1920.
	Serica brunnea (L.)	Sweden	Notini *et al.*, 1944.
	Silpha opaca L.	France	Danysz, 1894.
HYMENOPTERA	Hornet larvae	S. France	Friederichs, 1920.
	Sceliphron spirifex (L.)	S. France	Friederichs, 1920.
DIPTERA .	*Musca domestica* L.	S. France	Friederichs, 1920.
	Trichomyza fusca Meig. (= misspelling for *Teichomyza fusca* Macq.)	S. France	Friederichs, 1920.

February no living grasshopper could be found. Again, Williams (1921), who regarded the Green Muscardine fungus as the most important natural agent in the control of adult froghoppers, *Tomaspis postica* Walk., stated that its effectiveness depended on weather conditions. His artificial infection work in the field gave inconclusive results. Friederich's experiments were successful largely under conditions of high humidity and he concluded that attempts to produce epizootics would only be practical in

regions having a wet climate or season. In the present outbreak of the disease among the Eritrean locusts there is again correlation with warm wet weather as has been related above. Parthasarathy *et al.* (1953) successfully parasitised *Pyrilla* sp. with *Metarrhizium*, both in the laboratory and in the field, when the humidity was high. Wallengren (1929) showed that *Pyrausta nubilalis* succumbed to the disease in 12 days in slight atmospheric humidity; if the atmosphere was saturated, it succumbed in 6 days at temperatures of 16–19° C., and in 4 days at a temperature of 25° C. In passing, it should be mentioned that the minimum, optimum and maximum temperatures for the fungus in culture media are respectively: 10°, 25–30° and 32–34° C. Nirula (1958), in India, also fully confirms the significance of humidity for high infection in his records of the prevalence of the fungus in *Oryctes rhinoceros* L. between May and October, when the humidity is 70 per cent and the temperature 27° C. Moreover, he considers the prospects promising for the artificial initiation of epizootics in this insect, but the fact remains that this has not as yet been achieved. Other factors determining the pathogenicity of the fungus are (1) the condition of the insect—sick or injured individuals naturally succumb more readily to the disease; (2) the stage of the insect's development—certain stages are more resistant than others (Wallengren, 1931); and (3) the virulence of the fungus strain.

Control of the Fungus

Not only is there the problem of combating insects harmful to man and his crops, but there is also the reverse one of keeping beneficial insects, such as the silkworm and others required in a healthy state in insectaries, *etc.*, free from the disease, *i.e.*, the problem of exterminating the pathogenic fungus. Vago and Gingast (1954), working with another common entomogenous fungus, successfully infected several thousand silkworms with *Beauveria bassiana*. A portion of these had been fed on leaves dipped in 0·1 per cent. solution of neutral oxyquinolic sulphate and were kept in a breeding ground treated with the same solution. Of these, approximately only a half showed signs of infection, the chemical apparently having a therapeutic action. [An abstract only of this paper was seen; it is therefore difficult to assess the efficacy of this drug.] Vago and Hurpin (1954) recommended exposing equipment in use for insect breeding to formaldehyde vapour in a glass chamber for 8–10 hours, and that apparatus soiled by insect debris should be fumigated for 3–5 days. Glaser (1926) advised (1) removing all possibly parasitised silkworms, (2) examining their blood for fungal traces and destroying the infected worms before the fungus sporulates, and (3) regulating humidity.

Description of the Fungus

Metarrhizium anisopliae consists of hyaline hyphae (fungal threads) which penetrate the insect chitin by secretion of toxic enzymes and enter the body cavities. After loss of activity and subsequent death of the insect—generally in a few days—the tissues are invaded and the hyphae spread throughout the body, the corpse becoming hard and brittle. Eventually the fungus breaks outward through the skin, forming whitish cushions (sporodochia) which become green with the production of the reproductive bodies, or spores (= conidia). These latter are borne in chains on conidiophores arranged in a loosely penicilloid or brush-like manner. The spores vary in size in different strains of the species, ranging from 4·8–14 × 1·6–8μ. In the main, two forms have been observed, a large-spored form with spores 9–14μ long and a small-spored form with spores 5–8μ long. The measurements given by Delacroix (1893) covered the whole range, but generally the fungus can be relegated either to the large or to the small-spored strain. The latter is much the commoner. The locusts from Eritrea (1959) were affected by the small-spored form, the spores being 4–6 × 1·5–2μ. In the Northern Rhodesian epidemic reported by Lewin in 1936 and affecting the locust *Nomadacris septemfasciata*, again, a small-spored form was concerned, but

in this case the spores were consistently slightly larger, having a mean size 4·5–6·5 × 1·5–2·5μ. Whether the difference is to be related to the different host insect, and transference of the fungal strain to the other locust species in each case would effect a corresponding change in the spore size, is not known. Spores from both the Eritrean and the Rhodesian locusts, of which there are examples in the British Museum herbarium, were planted on peptone-glucose-agar but only the former developed, those from Rhodesia—24 years old—no longer being viable. The culture of the Eritrean fungus grew very readily, forming dark green colonies and the spore measurements in artificial media agreed with those on the host insect.

In conclusion it should be mentioned that, apart from some varietal names that have been created for certain strains which can perhaps best be regarded as physiological or biological races of the type of *Metarrhizium anisopliae*, two other distinct species have been described. The white *M. album* Petch, 1931, with a cerebriform stroma with the white conidiophores and spores forming a palisade, the spores measuring 3–4 × 1·75μ, occurred on *Tettigoniella spectra* on rice in Ceylon, and the brown *M. brunneum* Petch, 1935, on a *Cicadella* in the Philippines. This has a brown lax stroma with brown spores, 4–6 × 1·5–2μ.

Discussion

Summarising our knowledge of the Green Muscardine disease gleaned both from natural epizootics and from experimental work, it is evident that the pleophagic, cosmopolitan fungus responsible is able to produce infection only under conditions of relative warmth and high humidity, not merely because this is a general prerequisite for most fungal growth but because only under such circumstances are the spores able to adhere to the insect body long enough for them to germinate and penetrate the chitin and to initiate infection.

Consequently, pits in the ground designed to trap host insects can only serve as infection centres during periods of damp weather, and in addition the moisture content in the traps must be maintained at the requisite level to break surface tension between the fungus spores and their source of contamination, whether this consists of contaminated insects, foliage or soil, thus freeing them to become attached to fresh, clean insects. The spraying of crops and vegetation with spore-powder has no chance of a successful outcome if not followed by wet weather.

It is apparent that with the information at present available, it is no simple matter artificially to initiate large-scale infections in the wild where circumstances are very different from those of experimental trials. Were it otherwise, entomologists and pathologists generally would by now be much more conversant with this disease, and the causal fungus would be utilised far more frequently in combatting insect pests injurious to man and his works.

This leads to the question, what is it that can on occasion touch off a natural epizootic of this disease? Given a warm humid season, the universal presence of the parasite's spores which can develop rapidly and produce thousands more in 2–4 days, and the presence of suitable hosts, there would appear to be no reason why epidemics should not occur quite frequently instead of only occasionally as is the case. And why, in areas having a permanently moist climate, are not all the insects wiped out by this very common entomogenous parasite, once it has made a good start? Do insects possess some natural immunity so long as their environment is that to which they are perfectly adapted, and is it only if and when their normal conditions of life change that they become liable to infection? Perhaps, when the insect is thoroughly healthy, the minute fungal spores are unable to become attached or to break through the chitinous covering. Immunity experiments so far undertaken have not yielded much information. In connection with this, the possible presence of some defence mechanism has been postulated by some workers because when an " infection " does not " take ", a brown patch forms on the insect's body in the area treated.

The infrequency of epizootics cannot be accredited to a host specificity relationship of the *Metarrhizium* fungus. Such specificity of individual strains of the fungus has been postulated at times to account for non-infection of some species of insect, but on the whole the ease with which the fungus can be transmitted not only from one species of insect to another, but also from one order of insects to another, refutes this. This lack of specificity indeed prevents the fungus dying out in any one region.

Undoubtedly it is not a single factor but several inter-acting which keep the majority of insects in nature reasonably safe from infection and the species from extermination, and this even under circumstances very favourable to the parasite ; factors such as the health of the insect, its food, climate and surroundings generally, including freedom to go about its normal activities in an environment in which its parasites are not unalterably virulent and abundant, must play a large part in determining epidemics.

When one or more of these factors making for normalcy change, catastrophic disease may result, but only temporarily.

Conclusion

In conclusion, then, the fungus *Metarrhizium anisopliae* can be an effective agent in controlling (or damaging) insects in a confined space or in a relatively small area, given the prerequisite conditions. But it attains epizootic proportions only occasionally and only in particular natural circumstances. The prospect of the artificial production of epizootics for the extermination of large populations of insect pests is, up to date, not favourable. In addition to the risk of destroying, in the same operation, beneficial insects and the more obvious difficulties and vagaries of weather, insect biology and fungal virulence, there is the additional problem of the large-scale production of spore-powder, the keeping properties of which, should it not be immediately usable, are not great—certainly not without special methods of storage.

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NOTES ON *CHRYSOPS BICOLOR* CORDIER (DIPTERA : TABANIDAE) IN TANGANYIKA

By D. J. Lewis[1]

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The dissection and examination of flies that transmit disease often reveal not only the rate of infection but various facts about the state of the flies which provide useful information about their biology and relation to disease (Lewis, 1960). For instance, it has been found that in at least three species of *Simulium* nulliparous and parous flies have different biting cycles, in consequence of which the risk of infection with onchocerciasis and the result of observations on the infection rate depend on the time of day at which people are bitten or flies caught.

During studies on *Simulium* at Amani in October and November, 1958, females of *Chrysops bicolor* Cordier, which belongs to a group of three species easily recognised by their colouring (Oldroyd, 1957), were often caught biting man, and the opportunity was taken of making a few observations on them. Dissections were made of 127 flies, of which 35 were shown by the state of their ovaries to be parous. Various organs were examined in saline.

The Crop and Malpighian Tubes

The crop usually contained a clear liquid which was occasionally tasted and found to be sweet.

In *Simulium*, clarity of the Malpighian tubes is a sign of age ; the condition of these organs in *Chrysops* was not systematically observed, but it was noticed that the tubes of at least some parous flies were rather clear.

The Fat Body

Lavoipierre (1958) observed parts of the fat body of *C. silacea* Austen around the bases of the Malpighian tubes and in front of the rectum, and found that the fat body decreased as the eggs matured so that there was little left in the gravid fly ; he noted an extensive fat body in some flies which were at least ten days old and concluded that they might not have taken enough blood to cause ovarian development and that the material derived from the blood might have been stored in the fat body.

In *C. bicolor* there are two concentrations of central fat body in the abdomen, anterior and posterior. The former, to which attention was paid, is attached by tracheae to the midgut and to air sacs. In a nulliparous fly it is a conspicuous network of cells which are grey owing to the globules they contain. In parous flies the appearance of this tissue varies ; it has usually lost its reticulate appearance owing to shrinkage and has become clearer and less grey ; sometimes it is still net-like but contains brown areas or spots.

The Ovaries

An ovariole dissected from a captured nulliparous fly is shown in figure 1, and another, from which the sheath has been torn, is seen in figure 2. In each case the short terminal stalk is visible and is very different from the combined stalk and follicular relic of a parous fly (figs. 3–5). Figure 6 shows the size of a mature egg (1·20 by 0·24 mm. as compared with 1·00 by 0·30 reported by Duke *et al.*, 1956, for

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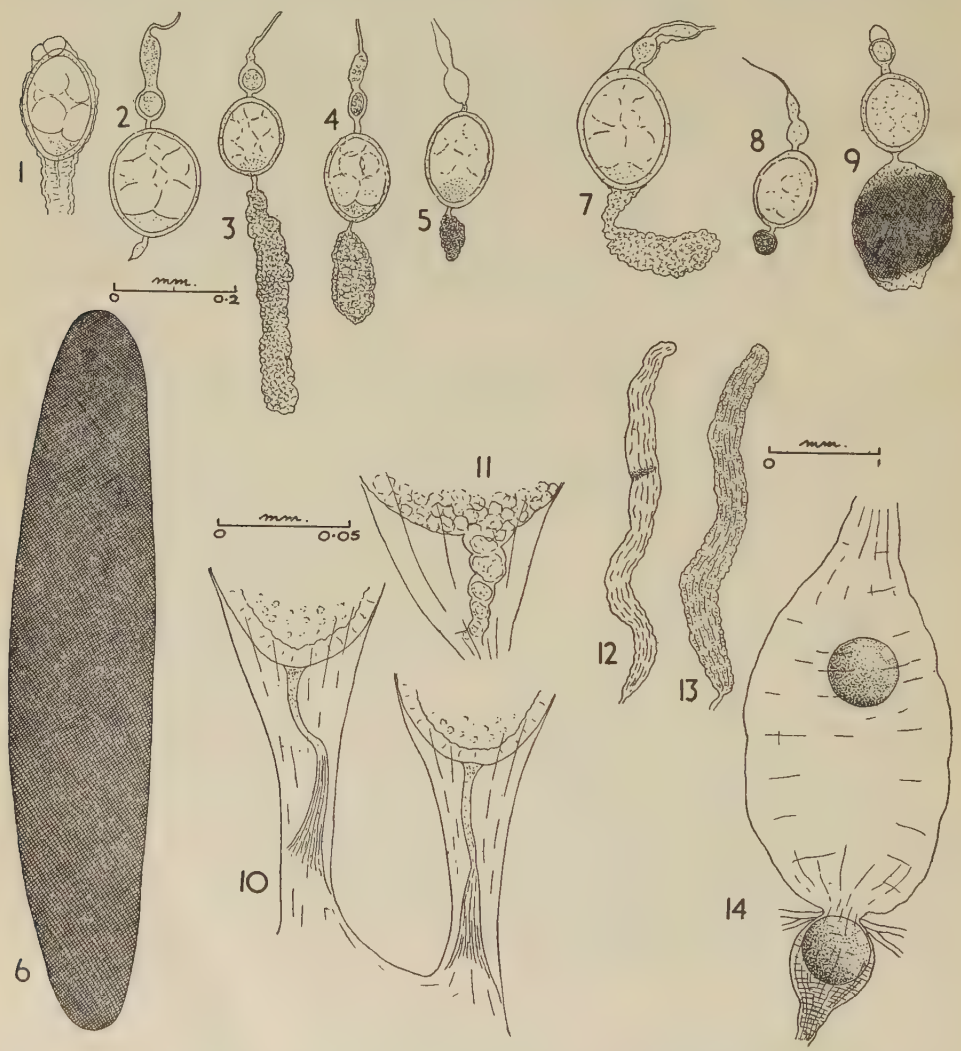
C. silacea), which gives an idea of the enormous expansion which the follicular epithelium undergoes before ovulation.

The follicular relics are useful for recognising parous flies, but careful observation is sometimes necessary. For instance, the ovariole sheath may lie in such a position that it hides the terminal stalk and looks rather like a follicular relic (fig. 7). Figures 8 and 9 show degenerated follicles, the smaller of which looks very like a small brown relic.

The appearance of posterior ovariole stalks of a nulliparous (fig. 10) and a parous fly (fig. 11) is of interest in connection with the way in which an egg is ovulated (Lewis, 1960). In the nulliparous fly the cellular structure of the stalks is not



Figs. 1–14.—Parts of *Chrysops bicolar* seen in saline after dissection : (1) Ovariole of nulliparous fly ; (2) another without ovariole sheath ; (3–5) ovarioles, without sheaths, showing follicular relics ; (6) ovulated egg ; (7) ovariole of nulliparous fly showing how part of sheath can simulate a follicular relic ; (8, 9) showing degenerate follicles, the former from same fly as (3) ; (10) two terminal ovariole stalks ; (11) stalk of follicular relic ; (12) accessory gland of nulliparous fly showing local opacity caused by secretion of globules following stimulation by a needle ; (13) accessory gland of parous fly showing general clouding due to remains of secretion ; (14) midgut and hind gut containing gregarine protozoan parasites.

obvious, but in the parous fly cells are clearly seen in the stalk attached to the posterior end of a relic and appear to have survived the passage of an egg through the relatively minute tube formed by the tunica.

Not more than one dilation of the tunica (representing an old ovulation) was seen in any one fly, but in a single instance brown patches were seen in the follicular relics and were presumed to be old relics surrounded by the new ones.

Relict eggs were seen in 14 per cent. of the parous flies, and they numbered from one to three with an average of 1·6. Duke *et al.* (1956) dissected a large number of *C. silacea* and found from one to six.

The Accessory Glands

Females of *Phlebotomus* have large accessory glands which expand and produce a visible secretion when the eggs are developing (Adler and Theodor, 1935, 1957 ; Adler, Theodor and Witenburg, 1938 ; Detinova, 1959 ; Dolmatova, 1942 ; Shoshina, 1951). After oviposition the glands, in some species at least, normally remain expanded and retain some of the visible secretion as evidence that they are parous. Garnham and Lewis (1959) examined the glands of several American species and found visible secretion in those of so many females that they suspected that it might appear in nulliparous flies before the eggs developed and so be of no use for indicating that a fly was parous. The large glands of *Chrysops* were examined with this question in mind.

According to Cragg (1912) and Patton and Cragg (1913) the accessory glands of *Haematopota* are long and tubular, with longitudinal folds, are composed of short cylindrical cells on a thin basement membrane, and, when fresh, contain a yellow granular secretion. The accessory glands of *C. bicolor* (figs. 12 and 13) have the same general appearance ; those of captured nulliparous flies are usually clear, and those of parous flies usually semi-opaque owing to the presence of globules of a sticky material. Dark patches of this were quite often seen in the glands of nulliparous flies, however, and investigations showed that they were the result of rapid local secretion caused by accidental pressure of a dissecting needle.

A Parasite

Gametocysts of a gregarine protozoan were often seen in the gut (fig. 14), either in the midgut or in the hind gut just behind the Malpighian tubes or in both sites. The cysts were present in 11 per cent. of the nulliparous flies, from one to three per fly, with an average of 1·7. They were seen in 11 per cent. of parous flies also, but only a single one was present in each of the (four) flies.

The cysts were grey spheres about 0·7 mm. in diameter and contained thousands of spores or oocysts each about 7 microns long, with terminal spines and containing eight sporozoites. The parasite bore some resemblance to *Lankesteria culicis* (Ross), the oocysts of which lack spines. The gametocysts of this species and of one found in *Chrysops silacea* by Beesley (1958) occur in the haemocoele, whereas the parasite of *C. bicolor* was always observed in the lumen of the gut.

Time of Biting

Some indication of the biting period is given by the combined hourly catches from 6 a.m. onwards for three days (20th–22nd November) : 0, 0, 2, 1, 9, 5, 3, 6, 6, 6, 5, 5. *Simulium* collected in the same place behaved quite differently, with well-marked morning and afternoon peaks of activity.

These and other catches gave no indication that parous flies had a different cycle from nulliparous ones, but more observations would be necessary to settle this point.

Acknowledgments

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SOME OBSERVATIONS ON TABANIDAE (DIPTERA) IN THE RUKWA VALLEY, TANGANYIKA TERRITORY

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Introduction

The Rukwa Valley, Tanganyika Territory, is a permanent outbreak area of the Red Locust, *Nomadacris septemfasciata* (Serville). The locusts live on the grass plains of the valley and it was thought that if these could be altered the locusts might be greatly reduced in numbers. In 1956, therefore, a small herd of cattle was introduced as a pilot scheme to determine whether or not cattle could be kept on the plains, as there was reason to believe that their presence in large numbers would materially affect the environment (Gunn, 1957). These cattle were seriously troubled by biting flies, particularly Tabanids, which were important both from their nuisance value and as possible mechanical carriers of disease. Gunn (1958) records that, in the cattle area, 27,000 unidentified Tabanids, probably mostly *Atylotus* spp., were collected in one day in five Harris traps.

Species

A total of 17 species was collected within the Rukwa Valley (*see* Table I). Of these, *Tabanus taeniola* P. de B. and *Atylotus* spp. were abundant at times and *Haematopota insidiatrix* Austen, *T. biguttatus* Wiedemann and *Dorcaloemus* spp. were seasonally common.

Distribution

The floor of the valley is covered by grass plains; these are surrounded by an area of grassed woodland in which *Acacia*, *Sterculia* and other trees are common. All the Tabanid species except *Chrysops fuscipennis* Ricardo were collected in the bush, but only five, *Haematopota brunnescens* Ricardo, *Atylotus agrestis* Wiedemann, *A. fuscipes* Ricardo, *T. taeniola* and *C. fuscipennis*, in the grasslands, and of these *H. brunnescens* and *C. fuscipennis* were isolated examples. The *Atylotus* spp. were most abundant on the plains, relatively few being taken in the bush.

Seasonal Abundance

Most of the species were present at some time during or just after the rainy season (Table I, fig. 1), relatively few occurring during the dry season. This agrees with the findings of Vanderplank (1944), and Glasgow (1946) also records peaks in Tabanid populations during the rains in other parts of Tanganyika.

Tabanus taeniola was taken in most months but was only common during the rains, being sometimes more abundant in December than any other species of Tabanid. Both Vanderplank (1944) and Glasgow (1946) give flight seasons of November to June, with a maximum in December, for this species.

They also record the various species of Pangoninae mainly in April and May, towards the end of the rainy season, and in Rukwa *Stenophora* spp. and *Dorcaloemus* spp. were only collected in these months.

Counts of the numbers of female *Atylotus* spp. on the plains were made by recording the numbers inside a Land Rover, with the sides of the hood rolled up, at 15-minute intervals. The flies were disturbed as little as possible so that each count is a record

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of a momentary level of a continuous infestation. The vehicle was always similarly exposed in grass about three feet high and entirely free of bushes or trees. The two species of *Atylotus* could not be separated because the flies were counted without being captured, but both species were common in collections from January to March, while only *A. agrestis* occurred in subsequent months (Table II).

Figure 1 shows the average number of *Atylotus* counted each month, together with the total monthly rainfall at one station in the 1955–56 rainy season. Numbers began to increase in December, reached a peak in May and then fell off steadily throughout the following dry season. In order to eliminate temperature effects, counts made at temperatures between 25 and 30° C. only are included in the figure.

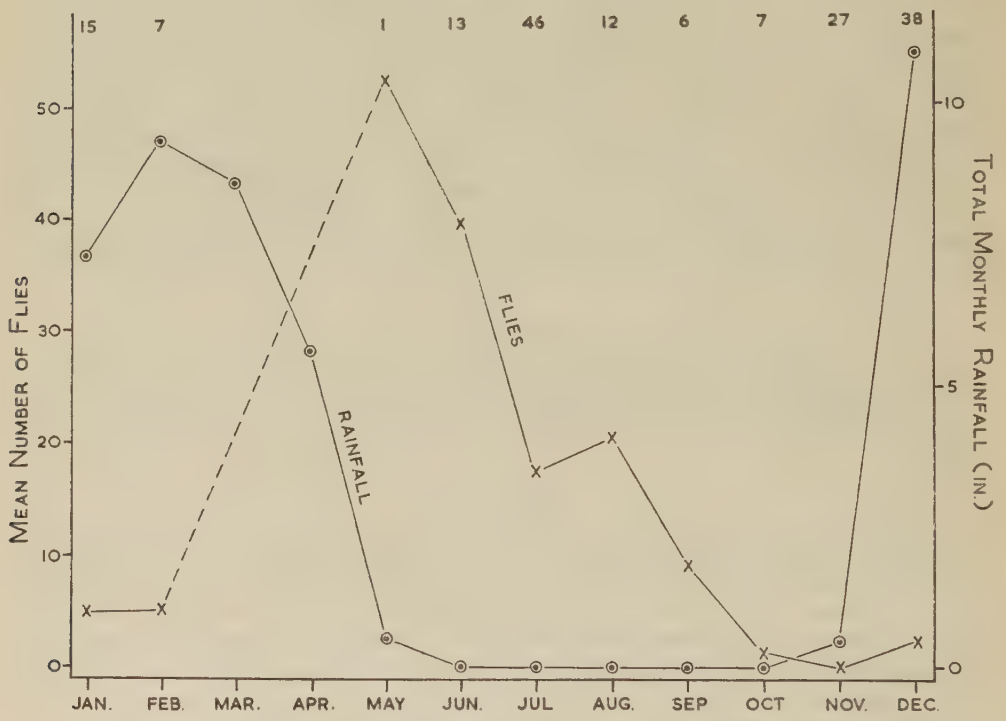

FIG. 1.—The average number of *Atylotus* counted each month and the total monthly rainfall. (The numbers at the top in figures 1 and 2 show the number of counts on which each point is based.)

ACTIVITY IN RELATION TO CLIMATE

During the 15-minute counts of *Atylotus*, air temperature and relative humidity were measured with a whirling hygrometer. Below 22° C. all the counts were zero, indicating that the flies were not active at these temperatures (fig. 2). Above 25° C. high numbers were generally present and further increases in temperature did not substantially alter the number of flies counted. There was, however, some variation in the temperature at which the flies became active. In June and July, with minimum overnight temperatures generally below 15° C., fairly large numbers of flies were active at 23° C. but in September, when the minima were around 20° C., very few flies were seen before the temperature reached 27° C. *T. taeniola* was also only occasionally seen at temperatures below 25° C.

The data do not show any relationship between activity and relative humidity or saturation deficit, but high wind reduced the number of flies, which appeared to cling to their footholds but finally to take off and be swept away.

TABLE I.—*The seasonal occurrence of Tabanids. Presence indicated by a cross* (×). (*Actual numbers are not given since they would have no meaning.*)

Species	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Haematopota denshamii Austen	×	.	.	.	.	.	.	.	.	.	.	.
H distincta f. *irritans* Oldroyd	×	.	.	.	.	.	.	.	.	.	.	.
H. brunnescens Ricardo	.	×	×	.	.	.	.	.	.	.	.	×
H. insidiatrix Austen	×	.	.	.	.	.	.	.	.	.	.	×
Ancala africana Gray	.	.	.	×	.	.	.	.	.	.	.	.
Euancala maculatissima maculatissima Macquart	.	.	.	.	×	.	.	.	.	.	.	.
Atylotus agrestis Wiedemann	×	×	×	×	×	×	×	×	×	×	×	×
A. fuscipes Ricardo	×	×	×	.	.	.	.	.	.	.	.	.
Tabanus insignis Loew	.	.	.	.	.	×	.	.	.	.	.	.
T. biguttatus Wiedemann	.	.	.	×	×	.	.	.	×	×	×	×
T. par Walker	×	.	.	.	.	.	.	.	.	.	.	×
T. taeniola Palisot de Beauvois	.	×	×	×	×	.	.	×	.	×	×	×
Chrysops fuscipennis Ricardo	.	×	.	.	.	.	.	.	.	.	.	.
Stenophora distincta Ricardo	.	.	.	×	.	.	.	.	.	.	.	.
S. zonata Walker	.	.	.	×	.	.	.	.	.	.	.	.
Dorcaloemus compactus Austen	.	.	.	.	×	.	.	.	.	.	.	.
D. silverlocki Austen	.	.	.	×	×	.	.	.	.	.	.	.
Totals	6	5	4	7	6	2	1	2	2	3	3	6

ACTIVITY IN RELATION TO TIME OF DAY

It was found that the activity of *Atylotus* increased in the mornings but decreased again in the middle of the day, reaching a second peak later in the afternoon (fig. 3). The mid-day depression of activity was not well-marked in July and August, but in September and October, when maximum temperatures up to 35° C. were experienced, the depression came earlier (11.00 and 10.00 hours) than in June, when maximum temperatures were less than 30° C. and activity reached a minimum at noon.

Morris (1934) and Nash (1937) record similar variation in activity in various species of *Glossina* in West Africa, attributing the reduction to tiredness or to the need to digest and to high temperatures. In *Stomoxys* sp. in Uganda, Coaker and Passmore (1958) regard the mid-day reduction in activity as a response to high saturation deficit, and Oldroyd (1957) suggests a similar cause for the reduction in biting, observed by Duke (1955), in *Chrysops silacea* Austen.

The morning increase in the activity of *Atylotus* was probably related to rising temperature and the final decrease in activity, late in the afternoon, to falling temperature, the flies being conditioned to high temperature at this time. Since, however, there was apparently no relationship between activity and saturation deficit, and temperatures were not always excessively high, the mid-day reduction in activity cannot be related to these factors. Saturation deficit was always greater in the middle of the day than at other times but was higher in July and August, when no marked

TABLE II.—*The percentages of* Atylotus agrestis *and* A. fuscipes *in catches made at different seasons*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Number collected	91	20	15	3	3	0	83	0	23	0	2	6
Percentage *agrestis*	69	5	53	100	100	.	100	.	100	.	100	100
Percentage *fuscipes*	31	95	47	0	0	.	0	.	0	.	0	0

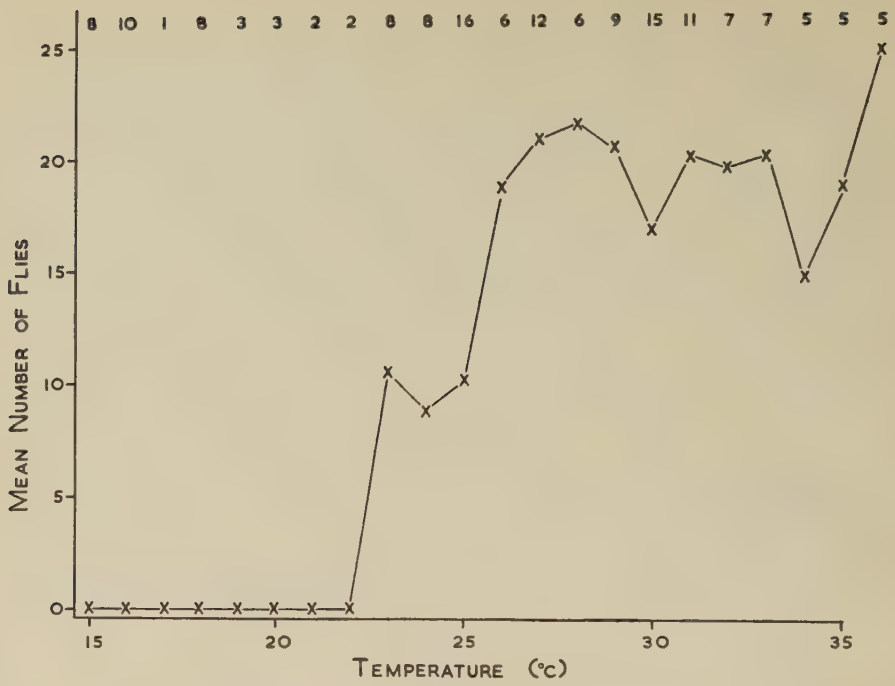

FIG. 2.—The number of *Atylotus* present in relation to air temperature, based only on observations made in July, August and September so that major seasonal differences are excluded.

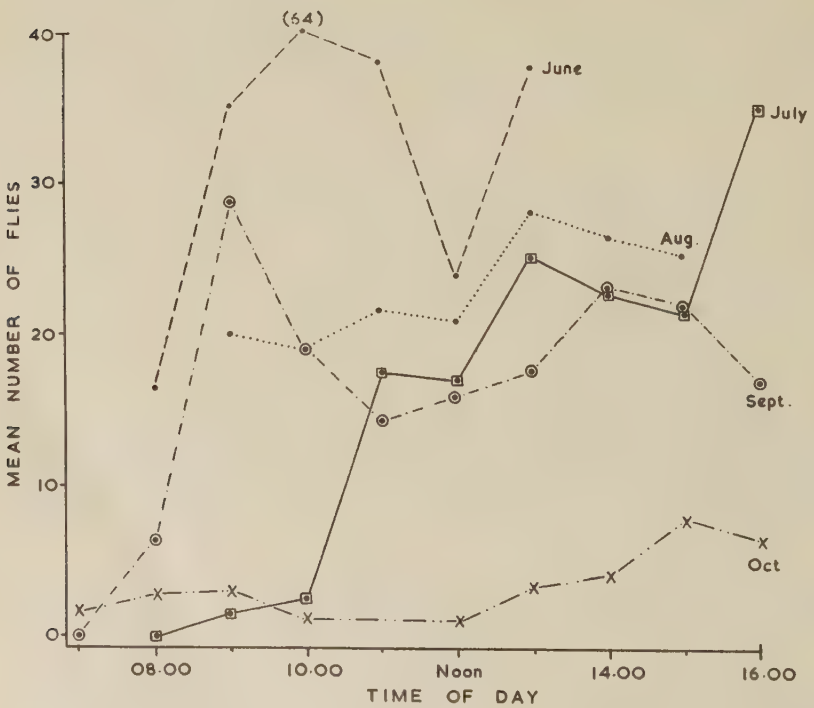

FIG. 3.—The number of *Atylotus* present at different times of day.

reduction in activity was observed, than in June, when a distinct reduction occurred. It is possible that the flies were active at times when the external conditions were changing, and became inactive when they were more stable so that the flies became conditioned to them (*cf.* Chapman, 1959).

Larval Cylinders

In the dry season in the Rukwa Valley all the rivers dry up and there is virtually no surface water on the plains except for the lake itself, and even this sometimes dries up. Normally the grass is burnt in July or August and the ground bakes and cracks. Soil temperatures of over 60° C. were recorded at this time, so that survival through the dry season must present a considerable problem to those species of Tabanid that pass this period as larvae or pupae.

In November 1955 a total of 15 mud cylinders made by Tabanid larvae (Oldroyd, 1954) were found in a dried-up pool. They had already hatched, but Mr. Oldroyd has suggested that they may have been produced by *T. taeniola*. The cylinders were found at distances of from three to twelve feet from the centre of the depression and it is presumed that the differences were related to their formation at different stages in the drying up of the pool. The length of the cylinders varied from 54 to 76 mm., the diameters from 23 to 32 mm. and the diameter of the exit hole from 5·5 to 7·0 mm.

The pool was a shallow depression, 18 × 24 sq. ft. in area, on the edge of the grass plains. It was peculiar in that no grass grew in it at any time although many other, apparently similar, depressions were characterised by the tall grass *Echinochloa pyramidalis*. When the pool was first found in November it was quite dry and the surface extensively cracked. Between the cracks the ground was very hard and a penetrometer exerting a force of 110 lb. per sq. in. did not break the surface. The top four inches of soil were honeycombed by small tunnels of unknown origin.

After the beginning of the rains the pool filled with water to a depth of about one foot. By February it was surrounded by *Echinochloa* but only water lilies and a water weed grew in the pool. In May it started to dry up again and was completely dry by June, when two more empty larval cylinders were found.

Summary

Seventeen species of Tabanid were collected in the Rukwa Valley, Tanganyika Territory. The commonest species were *Atylotus agrestis*, *A. fuscipes* and *Tabanus taeniola*, which were found on the grass plains. Most of the other species were confined to the fringing woodland.

Most species were commoner during or just after the rains than at other times, and *A. fuscipes* was only found from January to March, although *A. agrestis* was present at all times. *Atylotus* was not active below 23° C. and showed peaks of activity in the morning and late afternoon. *T. taeniola* was taken in every month except January, June, July and September.

Larval cylinders, possibly of *T. taeniola*, were found in a dried-up pool.

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I am most grateful to Mr. H. Oldroyd of the British Museum (Natural History) for his help and for checking the identifications.

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LABORATORY CULTURE OF *COELOPA FRIGIDA* (FABRICIUS) (DIPTERA: COELOPIDAE)[1]

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[Communicated by Dr. E. T. Burtt]

Introduction

The selection of a laboratory animal for genetical studies is largely guided by practical considerations of length of life cycle, number of offspring from individual pairs and ease of culturing. Where insects are concerned it is convenient if there is no diapause. *Coelopa frigida* (Fabricius) is a littoral acalypterate Dipteran of the family Coelopidae which breeds throughout the year in banks of seaweed cast up at high water mark (Remmert, 1955; Hennig, 1937). For several years it has been used in the laboratory of the Department of Zoology, King's College, Newcastle-upon-Tyne in a series of studies on morphology, genetics and embryology (Mayhew, 1939; Thompson, 1951; Bawady, 1954). The purpose of this paper is to give an account of the method of laboratory culture employed in current genetical work. The standard larval culture conditions were developed by U. Thompson, and adult culture conditions by B. Burnet, who has also extended Thompson's analysis of density and yield.

Culture Conditions for Adults

Adult flies are not known to undergo diapause. The length of the life cycle is 12 days at 25° C. The imagines are sexually mature 18 to 20 hours after eclosion. Mature females lay clutches of about 80 eggs at a time, and a single female may lay up to five clutches, although three is more usual. The last impregnation of the female is the effective one, so that substitution of a second male after a previous clutch does not result in mixed progeny. The second clutch cannot be fertilized for 12 hours after the laying of the first, so that females may be separated after laying and paired with a fresh male if desired. This has enabled Burnet (1958) to isolate recessive egg lethals directly, and to determine their allelic relations by crossing tested heterozygotes for a given lethal without recourse to visible chromosome markers. The survival of adults of a standard inbred laboratory strain on various carbohydrates is given in Table I. The carbohydrates were fed as 10 per cent. solu-

Table I.—*Survival of adult flies on various carbohydrates*

Substance	Days survival (until 50% dead) R.t.	25° C.
Water . .	4	5
Starch . .	4	5
Lactose . .	4	4
Dextrin . .	31	15
Sucrose . .	68	27
Maltose . .	64	34
Glucose . .	75	35
Mannitol . .	75	41

[1] This work was aided by a grant made available by the Department of Scientific and Industrial Research.

tions in a small reservoir and a cellosene pad moistened with sea water was also provided. The time of survival is taken as that up to which half the flies were dead. Fraenkel (1940) investigated the survival of *Calliphora erythrocephala* Meigen on various carbohydrates fed dry at 27° C. The results obtained with adult *C. frigida* are qualitatively similar to those for *C. erythrocephala*. Survival on glucose and mannitol appears to be rather better than on the other substances employed. In the wild state adult insects have access to mannitol which occurs in marine algae ; they are also observed to cluster on flowers near the shore.

Adult flies are stored in vials in a cold chamber at +5° C. and provided with a cellosene pad moistened with sea water and a reservoir of 10 per cent. mannitol solution. In this way flies of known genotype are stored to provide the backcross of parents to their children or even to their grandchildren. Fertile backcrosses are being made to grandparents about 30 days old, reckoning from the time of eclosion from the pupa. A protein meal is not normally required by adults for laying, but, in order to obtain successive batches of eggs successfully, each pair of flies is given a mannitol feed before being transferred to a new culture bottle. Flies which have already laid three batches, or which have been stored for long periods, are assisted with a killed yeast feed in addition to the mannitol solution. With careful culturing in this way it is possible to raise up to 300 offspring from a single pair of flies.

Culture Conditions for Larvae

In the wild, larvae feed within banks of cast seaweed which rapidly heat up through bacterial action to 20° C.–30° C. The heaps are composed of a heterogeneous mixture of algae, mostly Phaeophyceae with other marine rejectamenta. Most of the sites studied on the British North East Coast were composed of a mixture of *Laminaria* and *Fucus*, *Laminaria digitatum* and *Fucus serratus* predominating ; the relative proportions of each vary in space and time.

A standard larval culture medium suitable for genetical work was developed by means of a factorial analysis. Food materials consisted of : split stipe of *Laminaria digitatum*, 40 gm. ; fronds of *Fucus serratus*, 40 gm. ; and a mixture of *Laminaria* and *Fucus* consisting of 20 gm. of each. Additional materials consisted of 0·5 gm. fresh yeast and a pad of 3 gm. of cellosene moistened with 30 cc. of sea water. Cultures were raised in half pint milk bottles at 25° C. and constant illumination, with one pair of flies per culture.

The experiment was designed to determine whether any one food material could be used alone, and if either of the additional materials improved the yield. The experiment was randomised with several replicates for each combination. The results are summarised in Table II. *Laminaria*, cellosene, yeast combinations were found to be significantly better than other combinations. Inclusion of yeast in the medium improves the yield per culture, which agrees with the findings of Tatum (1939, 1941)

Table II.—*Factorial analysis of larval culture media*

Groups analysed for variance		Mean : flies per culture		Analysis of variance	
Combinations	Combinations			*F*	*P* (%)
With *Laminaria*	Without *Laminaria*	13·0	10·7	7·09	<1
With *Fucus*	Without *Fucus*	11·5	13·8	0·92	>5
With yeast	Without yeast	15·4	9·0	8·78	<1
With cellosene	Without cellosene	15·6	8·9	9·70	<1
Laminaria, cellosene, yeast	Rest	23·7	11·1	10·22	<1
Fucus, cellosene, yeast	Rest	20·6	11·5	5·29	5–1
Laminaria, *Fucus*, cellosene, yeast	Rest	18·3	11·7	2·70	>5

for *Drosophila melanogaster* Meigen. The inclusion of cellosene with sea water was also found to be beneficial, initially maintaining the high relative humidity within the cultures necessary for successful eclosion from the egg. Later the cellosene provides drainage for liquid released from the decomposing *Laminaria*.

Relationship of Yield to Larval Density

The mean yield per culture in the factorial experiment was poor because pairs of flies were allowed to lay several batches of eggs in each bottle. The relationship of yield to initial larval density was investigated in separate experiments using 40 gm., 60 gm. and 80 gm. of *Laminaria*. The regression lines for the three experiments are shown in figure 1, and a covariance analysis of the results in Table III.

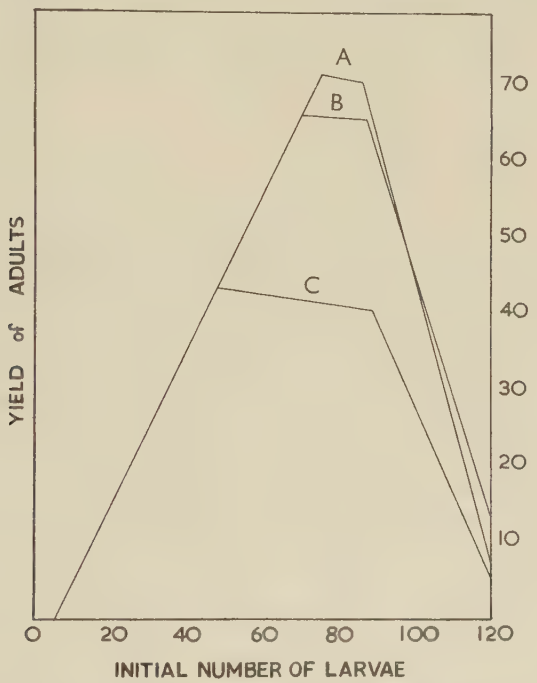

Fig. 1.—The relationship between yield of adults and initial number of larvae per culture. (*A*) 80 gm. of *Laminaria*, (*B*) 60 gm. ; (*C*) 40 gm.

For the first part of the graph the results for all three experiments are homogeneous, with an average regression coefficient, 1·023. Since it is slightly greater than unity, this coefficient indicates an increasing yield with increasing density. It may reflect the tendency of first instar larvae to feed in a group, usually on the medulla of the stipe. Adverse effects of undercrowding are discussed by Park (1933) and Allee (1934). The point of maximum yield differs between the three experiments, but the increase in yield is not in direct proportion to the amount of food supplied. The efficiency of yield measured as larvae per gm. of *Laminaria* is 1·1 with 60 gm., falling to 0·9 with 80 gm., and may be a function of the number of contacts between larvae with increasing density.

In the third part of the graph there is a rapid decrease in yield as initial density increases, and the regression coefficients are different for the three experiments. The regression lines are steeper as the food supply is increased. The reason for this, it is thought, is that with larger quantities of food larvae reach greater size before starvation, so that a proportionally greater accummulation of toxic decomposition products results from dead larvae.

TABLE III.—*Covariance analysis of density yield curves in figure* 1

	Expt. (gm.)	Mean yield	Covariance analysis for means: *F*	Covariance analysis for means: *P* (%)	Regression coefficient	Covariance analysis for regression coefficient: *F*	Covariance analysis for regression coefficient: *P* (%)
Initial increase of yield with density	40	36·0			+0·99		
	60	36·4			+1·04		
	80	36·5			+1·01		
			0·827	5		2·11	>5
Steady yield with increasing density	40	42·5			−0·08		
	60	65·8			−0·03		
	80	71·2			−0·12		
			1808·4	1		0·189	>5
Decreasing yield with increasing density	40	31·5			−0·82		
	60	53·0			−1·61		
	80	53·4			−1·85		
			209·9	1		34·52	<1

In all three experiments decreasing yield does not begin immediately after the maximum point, and there is a period of steady yield decreasing slightly (R.C. — 0·08) before the steeper part of the graph is reached. Maximum yield here is maintained in spite of increasing initial larval density because larvae reach the pupal stage at reduced body weight. It is found that with increasing larval competition reduction in body size of adult flies precedes reduction in the number of adult flies per culture.

It is possible to investigate the basis of size variability in Diptera from the knowledge that each microchaeta is produced by a single trichogen cell. Size differences between flies may be due to difference in the relative number of cells, or to difference in the relative size of cells, or to both these variables. The correct alternative can be distinguished by testing the relationship of a count of the number of microchaetae in unit area of wing surface to the size of the fly. In a standard wild type laboratory strain of *C. frigida* there is an inverse linear relationship on a logarithmic scale between the number of microchaetae per unit area of wing lamina and a relative measure of body size. The inverse relationship indicates that greater body size is due rather to larger cells than to an increase in their number, so that cell size in small flies from crowded cultures is smaller than that in larger flies from cultures with less larval competition. The severe decrease in yield which accompanies increase in initial density is thought to begin at the point when increase in initial larval density can no longer be accommodated by reduction in cell size and body weight. Vladimerova and Smirnov (1938) describe a reduction in mean pupal weight with increasing larval density in *Musca domestica* L. and *Phormia groenlandica* L., and Ullyet (1950) describes the reduction in pupal weight with crowding in sheep blow-flies.

DISCUSSION

The length of the life cycle, ease of culture and the number of offspring which can be raised from any individual pair of flies make *Coelopa frigida* a useful laboratory animal. As in *Drosophila*, the salivary gland chromosomes may easily be studied by use of a special technique (Philip, 1958; Philip, *unpublished*). The ability to make the cross of a female separately to more than one male, and to backcross parents to their offspring, is providing a useful tool in current genetical analysis.

The ecology of the Coelopidae poses many peculiar problems, as the family is exclusively littoral in habitat. The range of the genus *Coelopa* is global (Hardy, 1956), but that of *C. frigida* Palaearctic and Nearctic (Hennig, 1937), and *C. frigida* is distributed in a series of isolated and semi-isolated communities along the narrow

littoral zone. The peculiar nature of the habitat makes it of special interest to students of population dynamics, because defined communities of known size can be studied.

Remmert (1957) has found that populations of *C. frigida* from Heligoland differ from Baltic mainland populations both in nutritional requirements and in the minimal container size in which they will breed. Heligoland flies require a supply of animal protein in addition to brown algae for development, and a container not less than 12,000 cc. in volume, whereas flies from Kiel Harbour do not require animal protein and will breed in a container of about 1,600 cc. in volume. British North East Coast populations seem to resemble the Baltic populations in both these respects. Remmert's observations raise for the first time the problem of physiological races in *C. frigida*.

Acknowledgment

The authors particularly wish to express their thanks to Dr. U. Philip for the benefit of her advice and critical discussion throughout this work.

Summary

1. An account is given of the culture conditions employed for *Coelopa frigida* (Fabricius).

2. Adult flies are stored in a cold chamber at +5° C. with a pad of cellosene moistened in sea water and a supply of 10 per cent. mannitol solution.

3. Cultures of larvae are raised in half pint milk bottles on a standard medium consisting of 60 gm. fresh cut stipe of *Laminaria digitatum*, 0·5 gm. fresh yeast, 3 gm. cellosene wadding and 30 cc. sea water, at 25° C. and constant illumination.

4. Optimal yield, measured as adults produced per gm. of *Laminaria*, is given with 60 gm. of *Laminaria*.

5. The range of the species is described and its suitability for genetical studies discussed.

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TERMITES ATTACKING LIVING TISSUES OF *THEOBROMA CACAO* L. IN NIGERIA

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During a survey of the symptoms of *Calonectria* die-back on cacao trees in Western Nigeria, much of the dead wood and the adjacent living wood was found to be infested with termites. In one particular area over 25 per cent. of the dead branches were affected. The termites were identified as the dry wood termite, *Neotermes aburiensis* (Sjöstedt), by Mr. W. A. Sands of the Colonial Termite Research Unit. Further observations showed that the reproductive forms began their colony in the dead wood but, as the colony increased, adjacent areas of living tissue were often attacked. Nurseries were built in living wood and numerous galleries penetrated six to eight inches into living tissue; damage was often extensive, though never fatal to the tree. Two other termites, a *Coptotermes* sp. and a *Microtermes* sp. were found in dead cacao branches but these did not attack living wood. Termites have been reported infesting cacao in Nigeria as early as 1913 (Anon), but no identifications of termites attacking living wood are available. In French West Africa, Alibert (1951) reported *N. aburiensis* on cacao infesting dead wood in the neighbourhood of healthy wood and *Coptotermes sjostedti* Silvestri attacking dead wood.

A subterranean termite, *Macrotermes nigeriensis* (Sjöstedt), was observed to ring-bark seedlings, young trees and basal chupons on mature trees in cacao plots in many parts of Western Nigeria. Ring barking commenced at soil level and normally extended up to two feet above the ground. Less often, damage was observed 16 feet above soil level. Damage was seasonal, and was first observed at the beginning of the rains and was prevalent where coppiced trees had been "earthed up", where litter had accumulated close to the trunks of trees or where mulching treatments were applied. The damage frequently resulted in the death of chupons and seedlings and occasionally in the death of young trees.

The termite galleries of *N. aburiensis* when infesting cacao trees passed through the zone between the dead and living wood, where the die-back fungus *Calonectria rigidiuscula* (Berk and Br.) was active, and there was a possibility that the termites carried this fungus ahead of its usual position. Die-back is sometimes arrested in the tree where side branches, twigs or even leaves grow out from the diseased branch and were the fungus carried past these barriers by termites, it would constitute a serious problem. Cultures, made from living wood taken from the sides of these galleries, did not yield the die-back fungus and it was therefore considered unlikely that the termites spread infection.

Termites cannot be ranked as important pests of cacao, but in certain areas of Nigeria control would seem desirable. Control of *N. aburiensis* could be achieved by pruning off all the dead branches to prevent infestation. This would, at the same time, control the *Coptotermes* and *Microtermes* species attacking dead wood. Nests of *Macrotermes nigeriensis* should be destroyed in the vicinity of the cacao trees, and where infestation is particularly heavy, the use of a soil insecticide is recommended.

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THE BRITISH DISTRIBUTION OF THE WATER-BUG *VELIA SAULII* TAMANINI WITH SOME NOTES ON ALARY POLYMORPHISM

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Most collectors regard *Velia* as an inhabitant of small, fast-flowing streams and so most records of the genus refer to *Velia caprai* Tamanini, which occurs in large numbers in such situations.

Velia saulii Tamanini was first recorded from Britain by Brown (1951), and most records published then and since are of very small numbers of insects (Brown, 1954). These were usually found on larger bodies of water than those inhabited by the commoner species, many of the records being from lake shores. In a recent account of the vice-comital distribution of *Gerris* and *Velia* species, the author (1959) described several new loci, and in each instance *V. saulii* was found beneath large stones on the shores of lakes and large rivers. A large population was found in just such a situation on the shores of the River Conway at Llanrwst on 12th July, 1959. The collection was made on the Caernarvonshire side of the river, but the species undoubtedly occurs on similar shores on the Denbighshire side, as it was present in large numbers and winged forms were observed. This is the first known locality in North Wales, and it is suggested that a few minutes collecting in such situations would yield many further records.

Although few individuals are enumerated in my own published records the species was frequently abundant in typical habitats, this being especially true of the shores of Lake Windermere, where many individuals have been observed on subsequent occasions. All my collections to date, amounting to at least a hundred specimens, have been of the apterous form, but the Welsh population comprised not only 13 males, 18 females and innumerable fifth instar nymphs, all apterous, but also 2 long winged females. Long winged forms are relatively abundant on the River Derwent, Co. Durham (H. B. N. Hynes, *personal communication*), and at St. Mary's Loch, Selkirk (Brown, 1951); most other records of this form are of single individuals, possibly solitary migrants. The evidence thus accumulated does not seem to support the view that long-winged forms are any commoner in *V. saulii* than in *V. caprai*. In the latter species most populations are entirely apterous but some on the Silverburn in the Isle of Man and on some streams in the Lake District frequently contain long winged forms. Other streams in these areas yielded entirely apterous populations.

One can probably assume that all the Gerroidea were originally winged but had a strong tendency to polymorphism. The genetics of this polymorphism in *Gerris* have been discussed by the author (1960) and may be summarised as follows. The *AA* genotype is lethal, the *Aa* genotype produces always a short winged phenotype, and the *aa* genotype results in a phenotype which may be long-winged or short-winged, according to an environmental factor. This factor appears to be the ambient temperature at the time of vitellogenesis and in the author's opinion there is a critical temperature such that *aa* eggs which have undergone vitellogenesis at a higher temperature produce long-winged forms, but when vitellogenesis takes place below the critical temperature short-winged forms result. Such genetical " switch-mechanisms " are known in *Gammarus duebeni* Lillj (Kinne, 1953).

In most species the gene *A* has been eliminated. In univoltine species the critical level of the environmental factor involved will presumably be such as to produce either an almost uniformly long-winged or a short-winged population. Selection has favoured the maintenance of apterous populations on rivers and streams

(*Gerris najas* (Degeer), *Velia* spp.), and macropterous populations on ponds (*G. costae* (Herrich-Schaeffer), *G. gibbifer* Schummel), but apterous populations, consisting of small individuals dwelling in ponds, of *Microvelia* and *Hydrometra*. The rare alternative forms observed in these species could be produced by unusual local conditions or, if the thresholds of the environmental factor are normally distributed, they might represent those "tail" individuals responding to ordinary environmental conditions by producing the more unusual form. On the other hand, a combination of these two factors could operate. It may be significant that I caught my first (British) winged *G. najas* (a sub-macropterous female) during the exceptionally warm summer of 1959 from a population in which I have observed many thousands of wingless individuals.

The rare alternative forms of these predominantly monomorphic water-bugs are known often to be of local occurrence, viz. *Velia* (see above) and *G. najas* in the Pyrenees. Some workers, notably Poisson (1924) and Sprague (1956), have carried out breeding experiments on these species, and found that the common form bred true under varying conditions, whereas the rare form usually gave rise to mixed populations. In the latter the parental form was present in greater abundance than in natural populations, although still by far the rarer.

These observations, which indicate that the rare forms are not simple mutants, are in accord with the hypothetical possibilities outlined above. Much further work is required before a uniform theory of the determination of polymorphism in water-bugs can be formulated, but at present there is no reason to suppose that this will be very different from that proposed for polymorphic *Gerris* species (Brinkhurst, 1959*b*).

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—— 1936, New species of Coccidae. *Trans. R. ent. Soc. Lond.* **84** : 901–36.

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TO BE HELD IN THE SOCIETY'S ROOMS
41, Queen's Gate, S.W.7

1960

Wednesday, October 5
„ November 2
„ December 7

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